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THE BOTANICAL REVIEW

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THE EFFECTS OF FLUCTUATIONS IN WEATHER UPON THE GRASSLANDS OF THE GREAT PLAINS

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INTRODUCTION

Scope of Review

The purpose of this review is to discuss the effects of fluctuations in weather upon the native steppe grasslands of the Great Plains of North America. While the conflicting reports of early expeditions suggest, and the experiences of settlers confirm, that variations in weather are characteristic of the region, detailed information concerning their effects on the native vegetation has been obtained only during the past third of a century. Previously quantitative methods of measuring grassland vegetation were in the developmental stage, and the number of grassland investigators was small. Since stands of undepleted native vegetation were still abundant, study in the early part of the century was concerned with the characteristics of the plant cover without much consideration to the extent of change from causes other than overgrazing. The possibility of major changes in floristic composition resulting from variations in weather was probably discounted because of the long-lived perennial habit of the climax dominants. In supporting the theory that the vegetation was in equilibrium with the climate, some workers may have minimized the extent of variations possible.

Following the start made in Nebraska by Pound and Clements (1898), studies of the native grasslands of the Great Plains were continuing at the time of the inception of widespread drought in 1933, thus presenting an opportunity to examine the effects on the vegetation of this eight-year catastrophe. While many of these investigations were originally designed to study the influence of grazing animals, reaction to drought could often be separated because of its major effects and the presence of a moderately grazed or ungrazed treatment in the experiment. It is upon the reaction to the drought of 1933-40 that this review is mainly based. In this connection the work of J. E. Weaver of Nebraska and F. W. Albertson of Kansas is classical because of the detail of their observations over extensive areas throughout a period of more than three decades. Additional information has been obtained in the same areas during the present drought (1950—). Since this drought has not spread to the northern grasslands, it has recently been possible in Canada (Coupland, 1958) to describe some of the responses of the vegetation to an extended period of above-average moisture conditions.

Description of the Region

Considerable disagreement exists concerning the northern and eastern boundaries of the Great Plains. It is agreed that the area is bounded on the west by the Rocky Mountains and that it extends southward to the vicinity of the Rio Grande (about 30° N. Lat.) in western Texas. Atwood (1940) considers that the region reaches northward to the delta of the MacKenzie River just beyond the Arctic Circle, while the Canadian concept is that it extends only to the southern boundary of the Northwest Territories (Mitchell and Moss, 1948). The matter has been further confused by the popular concept of the coincidence of the northern boundaries of the grassland plant formation and the Great Plains physiographic province. Many American writers consider the "Northern Great Plains" to extend southward from the Canadian border or from a position slightly to the north of it (Allred, 1940; Rogler and Hurtt, 1948). The "Southern Great Plains" is variously considered to lie southward from the South Dakota—Nebraska line (Weaver and Albertson, 1956), the Nebraska—Kansas line (Savage *et al.*, 1948), or the Kansas—Oklahoma line (Thorp *et al.*, 1948).

Delineation of the eastern boundary is particularly difficult. The American physiographers, Fenneman (1931) and Atwood (1940), agree that the division from the Central Lowlands to the east should be made by a line joining certain distinct physiographic features—the Red Hills of Texas and Oklahoma, the Plains Border of Kansas, and the Missouri Coteau of North Dakota and southern Canada. The Canadian concept (Mitchell and Moss, 1948) locates the eastern edge at the Manitoba escarpment (98—99th Meridian) which agrees with most American writers (Allred, 1940; 1945; Whitman and Stevens, 1941; Rogler and Hurtt, 1948) who consider the Great Plains as extending east of the Missouri Coteau to the western edge of the Red River Valley in North Dakota. Many arbitrary limits have been used to mark the eastern boundary, including the 15- and 20-inch isohyets, the 1500- and 2000-foot contour lines, and the 97th, 98th and 100th Meridians. For the present purpose the boundary suggested by Fenneman (1931) and Atwood (1940) is adopted as far north as the South Dakota—North Dakota line and then a more easterly boundary is used, following along the western edge of the Red River Valley and the western shores of glacial lake Agassiz between the 98th and 99th

Meridians (Figure 1). This definition agrees closely with boundaries of vegetation types (Whitman and Stevens, 1941; Weaver and Bruner, 1954) and climatic characteristics (Livingston and Shreve, 1921; Thornthwaite, 1941).

The northern portion of the Great Plains is principally forested (Moss, 1956) and is not considered here. The main body of grassland extends about 275 miles into Canada (Coupland, 1950; Moss, 1956), where it gradually gives way to forest in the aspen-grove region, a zone up to 100 miles or more in width (Moss, 1932, 1944, 1956; Moss and Campbell, 1947; Coupland, 1952; Coupland and Brayshaw, 1953). Isolated areas of prairie occur even within the forest region north of this tranisition zone (Moss, 1952) but will be omitted here together with the fescue prairie of the aspen-grove area because of lack of data concerning fluctuations of the vegetation in these areas.

The area involved comprises about 600,000 square miles in the United States, while the grassland area included in Canada approximates 100,000 square miles. The width of the area is nowhere much less than 400 miles and its length 1600 miles.

PHYSICAL FEATURES. The diversity of topographic style has caused Fenneman (1931) to divide the area into ten sections, the largest and most uniform of which are the High Plains of the south and the Missouri Plateau of the north. Although vast stretches are conspicuous in their lack of pronounced relief, several major physical features occur. The most prominent of these are the Black Hills of South Dakota and several other smaller outliers of the Rocky Mountains in the northern part, sandhills (particularly in Nebraska where 18,000 square miles are involved) and extensive areas of badlands, particularly in South Dakota.

The elevation of the area along the foothills of the Rockies ranges from an average of 5,500 feet above sea level in Colorado to less than 4,000 feet in southern Alberta. The slope is generally toward the east, being about a ten-foot fall per mile and reaching 1,500 feet elevation along the eastern margin (Atwood, 1940; Mitchell and Moss, 1948).

GEOLOGY AND SOILS. The deposits upon which the soils have been formed consist of sandstone, limestone, shale, lignite and conglomerates which have been modified by erosion and deposition activities of water, wind and ice. "Nowhere else . . . are there more

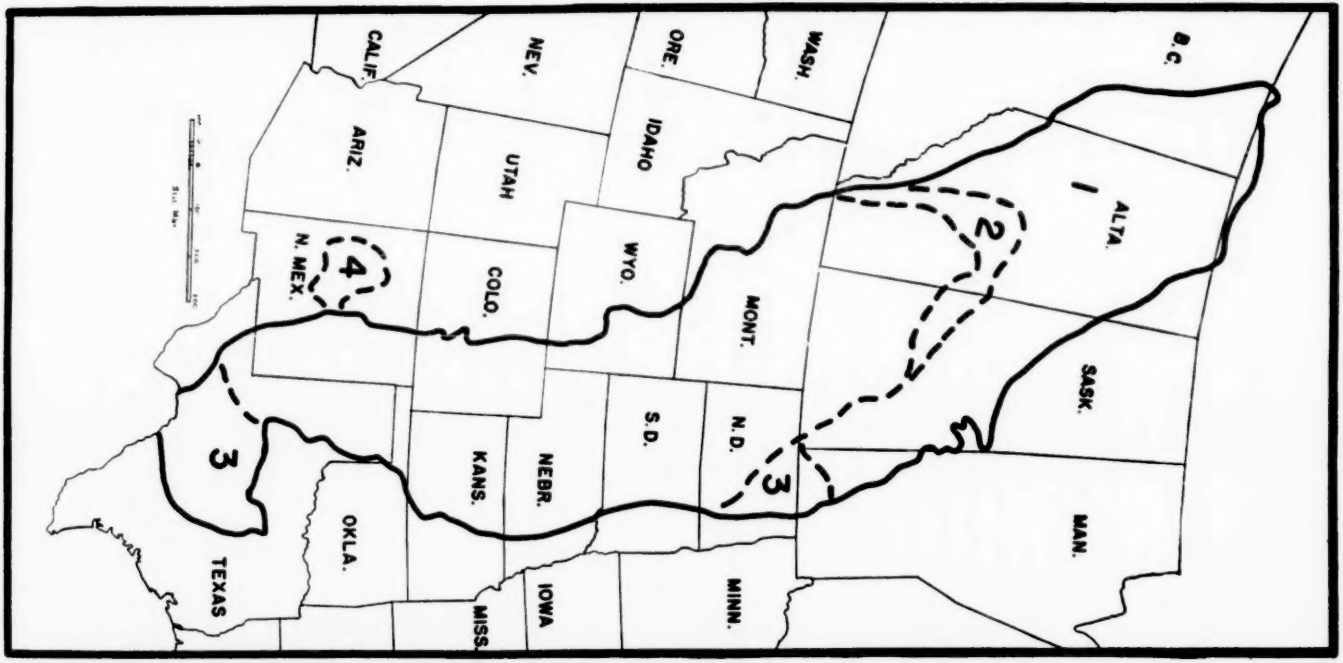

Figure 1. Outline map of the central United States and southern Canada showing the boundary of the Great Plains (solid line). The boundary of the Mixed Prairie coincides approximately with that of the Great Plains except where indicated by the broken lines: 1=forest; 2=Aspen Grove—Fescue Prairie region; 3=True Prairie within the Great Plains; 4=Mixed Prairie outside of the Great Plains.

remarkable examples of extensive alluvial fans that have blended and formed a vast alluvial plain at the base of a mountain region. Nowhere else are more symmetrical examples of consequent drainage to be found" (Atwood, 1940). In the Canadian portion and in northern Montana and North Dakota recent glaciation has left morrainic deposits (Fenneman, 1931; Edmonds, 1944; Thorp *et al.*, 1948; Ives, 1950).

Brown and chestnut soils occupy most of the region, the former being associated with the more arid conditions near the mountains. With decreasing aridity eastward, chernozem soils are found from Kansas northward along the eastern margin of the Plains. In parts of Oklahoma, Texas and New Mexico there are reddish chestnuts. Along the foothills and in mountain outliers the westward trend towards aridity is reversed, and isolated zones of chestnut or chernozem soils occur within the brown soil zone. Because of sorting by wind and water, there is a wide range of textures from the heavy clay of former lacustrine areas to the sand of dunes (Lyon and Buckman, 1946; Mitchell and Moss, 1948; Thorp *et al.*, 1948).

CLIMATE. The climate is considered by Thornthwaite (1941) to be dry-subhumid to semiarid. The precipitation increases with increasing distance from the Rockies, averaging less than 20 inches annually except in the warmer southern portion where it reaches 27 inches (Bruner, 1931). In parts of the region more remote from the influence of moist air from the Gulf of Mexico, the annual precipitation averages less than 12 inches. The mean annual temperature decreases northward from 65° to 34°F. in January the mean ranges from 50°F. in the south to about 0°F. in the north. Growing season temperatures are more similar, the mean for July in the south (80°F.) being only 20°F. higher than in the north. Higher rates of evaporation occur in the warmer areas, the mean for the growing season ranging from 60 inches in the south to 25 inches in the north. The average length of the frost-free season decreases northward from over 200 to less than 100 days, while the average depth of frost penetration increases from one to over 50 inches. The climate is windy, particularly in the spring. The average ratio of precipitation to evaporation is about 0.60 along the eastern boundary and decreases westward (Livingston and

Shreve, 1921; Kincer, 1941; Thornthwaite, 1941; Kendrew and Currie, 1955; Weaver and Albertson, 1956).

VEGETATION. The boundaries of the grassland portion of the Great Plains as defined above coincide roughly with those of the main body of the Mixed Prairie (*Stipa-Bouteloua*) Association as defined by Clements and his associates (Weaver and Clements, 1938; Clements and Shelford, 1939) (Figure 1). The climax is comprised of a mixture of mid and short grasses. The major genera are *Agropyron*, *Aristida*, *Bouteloua*, *Buchloë*, *Hilaria*, *Koeleria*, *Sporobolus* and *Stipa*, while *Carex is* almost always associated with the grasses. Distribution of species varies markedly in different parts of this vast vegetational unit but the major species are found practically throughout.

Allred (1945) considers it probable that present-day grasses are "descendants of some primitive fescue which evolved from sedge-like ancestors in the Cretaceous geological period". The Plains gradually became dry during the Cenozoic era because of uplifts associated with the retreat of the Cretaceous sea and the interception of moisture-laden winds by the newly-formed Rocky Mountains. This resulted in the destruction of the warm temperate forest of the Eocene. Following a period of building up of the Plains by deposition of fluvial materials from the mountains by rivers and streams, the Mixed Prairie probably originated about 25 million years ago. Records of modern grass genera in Miocene strata and the record of adaptation of the teeth of animals support this period of origin of prairie (Clements, 1936; Clements and Chaney, 1937; Elias, 1935, 1942). Clements and Shelford (1939) have concluded that the mid grasses are of both northern and southeastern derivation, depending on their cool-season or warm-season characteristics, while the short, drought-resistant species arose in the arid zones of Mexico and Central America. Intermingling of these groups of species throughout the Great Plains took place during the climatic pulsations of glacial times.

Previous to settlement in the middle of the nineteenth century, the principal disturbance was caused by grazing animals. Clements and Chaney (1937) are of the opinion that the combined effects of bison, antelope and deer, and of wild horses and cattle, before settlement was always less than supposed, being limited to a tem-

porary harmful coaction upon the mid grasses with corresponding advantage to the short grasses. The view of Albertson *et al.* (1953) is not necessarily opposed to this when they state that at least moderate use of the grassland by bison was common.

After settlement began, overgrazing of the vegetation resulted in the formation of a short-grass community (disclimax) which has been often taken to represent the natural condition. However, the evidence seems conclusive that the climax is a mixture of mid and short grasses (Clements, 1920).

The Mixed Prairie extends westward beyond the Great Plains into northern New Mexico. Similarly, the True Prairie (*Stipa-Sporobolus*) occurs within this physiographic unit in northeastern North Dakota and southwestern Manitoba in the north and in an eastward extension of the Great Plains in central Texas in the south (Whitman and Stevans, 1941; Clarke *et al.*, 1942; Coupland, 1952). Here the moisture relationship is sufficiently favorable to permit the mid grasses to exclude the short grasses as dominants (Figure 1).

LAND UTILIZATION. Settlement of the Great Plains has been greatly influenced by the aridity of the climate. Cattle ranching began in the south in the early part of the last century but was delayed in the north until about 1875. Spread of farming into the region from the east was impeded by the early description of the area as the "Great American Desert". After settlement started about the middle of the century, the droughts of 1860-62, 1870-73, 1883-89 and 1893-95 impeded farming and resulted in emigration from the Plains. Not until methods of dryland farming were perfected (1885-90) was it clear that the Great Plains would be used for crop production.

Following the Civil War the shortage of cattle in the northern States resulted in expansion of the cattle industry throughout the Plains. The relief of grazing pressure on the vegetation caused by the slaughter of the buffalo was thus soon made up by an increasing population of domesticated livestock. With the spread of dryland farming as far west as the brown soils by 1890, overstocking of the uncultivated land occurred. Overgrazing and adverse prices were added to drought as factors in checking expansion. After the drought of the 1890's the enthusiasm for dryland farming returned

with the climatic risks recognized. The drought of the 1930's brought about the end of this second period of expansion (Webb, 1931; Clements and Chaney, 1937; Thomson *et al.*, 1938; Woestemeyer and Gambrill, 1939; Hafen and Rister, 1941; Kirk, 1941; Rule, 1941; Clarke *et al.*, 1943; Dick, 1943; Cardon, 1949; Strange, 1954).

In this semiarid climate low soil moisture supply is the most important factor limiting crop production. According to Allred (1940), 63 per cent of the portion of the Plains south of the Canadian boundary is grazing land. The distribution of cultivated land is not uniform. The more intensively cropped areas are in the eastern districts on dark soils where 80 per cent of the area is cultivated in some counties. In the west the cultivated portion is sometimes less than one per cent (Rogler and Hurtt, 1948). The fluctuating livestock population probably numbered over 15 million animal units after the drought of the 1930's (Allred, 1940; Clarke *et al.*, 1943). Grazing capacities average about two acres per animal unit month in the east to four acres in the west, but on poorer ranges may be as much as ten acres (Clarke *et al.*, 1942; Hurtt, 1948). Overgrazing in vast areas has reduced the productivity so that one-third of the range area in the northern States is now producing only 60 to 80 per cent of the forage possible under good management (Hurtt, 1948a). Similar deterioration is evident elsewhere.

Non-agricultural industry, while developing, is not extensive. The development of mineral resources is highlighted by the occurrence of oil, coal and salt fields in various areas. Manufacturing of building materials is also an important pursuit. This agricultural economy supports a sparse population of about six persons per square mile, 60 per cent of whom are urban dwellers (Rogler and Hurtt, 1948).

FLUCTUATIONS IN WEATHER

In the semiarid Great Plains wide climatic fluctuations are to be expected (Thornthwaite, 1941). Borchert (1950), in his excellent work on "The Climate of the North American Grassland", has shown that a great drought east of the Rockies is likely to be most severe in the grassland. He states further that "droughts east of the Rockies have tended to occur when, and where, there has been a

movement of dry, continental air eastward from the base of the Rockies. The farther eastward a flow of this dry air has extended, the farther east the drought has extended. The stronger the westerlies over the United States, the more extensive the drought area east of the Rockies. This has been shown for short periods and for long periods; it is a phenomenon observable in the climatic records for periods of a few days or for many years; and it has been shown in a variety of studies of weather and climate".

Borchert suggests that the climate increases in aridity westward due to the stronger, more incessant flow of air off the mountains. He found that all of the Mixed Prairie receives a mean transport of air from the eastern base of the Rockies for 12 months of the year, while there is a rapid transition towards a decrease in this value to the northeast and southeast. Ives (1950) considered the effects of Chinook winds in modifying the climate to the immediate east of the Rockies. He concluded that they have a negligible influence on the annual climatic averages, so that it seems that the general circulation is the important factor.

Investigations by the Carnegie Institution of Washington have shown that variations in climate are cyclic and bear a close relationship to the sunspot cycle. Douglass (1919) found a correlation between dates of minima and maxima tree growth, rainfall, temperature and solar phenomena. Practically all trees investigated showed the sunspot cycle or its multiples. Other studies (Clements, 1921, 1929, 1938; Clements and Chaney, 1937) revealed that at each sunspot maximum of 80 numbers or more (1860, 1870, 1893, 1917), droughts of two to four years occurred in the Great Plains, while shorter periods of drought were coincident with abrupt changes in number of sunspots towards either the minimum or maximum.

In addition to deficient annual percipitation, many other weather factors inhibit plant growth in the Great Plains. These include evaporating power of the air, inopportune distribution of rainfall, hailstorms, wind and soil blowing (Chilcott, 1927).

Precipitation

According to Thornthwaite (1941a), almost everywhere the driest year brings less than ten inches of precipitation, the rainiest more than three times as much. He has shown that at a dry sub-

humid station, like Jamestown, North Dakota, the climate was actually moist subhumid in 15 years out of 35 and humid in one, while in five years the climate was semiarid and in one arid. Tannehill (1947) has found that there has been a tendency for great rainfall deficiencies east of the Rockies to be concentrated in relatively few years and to be widespread during those years. The years most commonly considered to be "great drought years" since weather records were regularly taken by a network of stations are 1890, 1894, 1901, 1910, 1917, 1930, 1933, 1934 and 1936 (Henry, 1930; Hoyt, 1936; Borchert, 1950). These workers might also consider some of the more recent years, particularly 1956, in this category. Localized drought has been more frequent (Campbell, 1936; Visher, 1949).

The fluctuations in annual precipitation, while marking the major periods of deficient and sufficient precipitation, fail to allow for variations in distribution which occur during the year. Anywhere in the Great Plains the collision of moist tropical air with dry polar air may result in such heavy precipitation that as much as a third of the average annual precipitation may occur in one day, and a fifth in a single hour. Since these invasions and interactions are rare, there may be periods as long as 120 days without rain. The drought hazard is greatest in winter and least in late spring and early summer. "Drought periods of 35 or more consecutive days may be expected annually and periods of between 60 and 70 days once in 10 years. Less frequently a drought period may reach 90 days in the northern Great Plains and 120 days in the southern Plains. The drought hazards in autumn and winter are approximately equal in the central and northern Plains, but in the southern Plains the winter hazard greatly exceeds that of any other season. Throughout the Plains prolonged periods of drought are least likely to occur in summer" (Thornthwaite, 1941a).

The term "drought" has usually not been accurately defined. Some (Shantz, 1927; Barger and Thom, 1949; Van Bavel, 1953) have emphasized that moisture must be deficient for plant growth throughout the period considered as a drought. However, more frequently the total time between periods of precipitation has been included (Blumestock, 1942). Henry (1931) considered the total annual precipitation to be a satisfactory measure to fix the times and places of drought. He concluded that in the Great Plains

any one year when the precipitation for a State is 65 per cent or less of average may be considered as a year of extreme drought. Such a condition existed in northwestern Oklahoma for a four-year period (1951-55) during the most severe drought on record (McIlvain *et al.*, 1955). Several workers have pointed out the occurrence of drought years in groups (Henry, 1931). Hurtt (1951) considers that in eastern Montana drought has occurred on the average of one year in five over a 60-year period. Some workers (Blumstock, 1942; Barger and Thom, 1949a) have discussed methods of evaluating the probability of occurrence of drought.

Periodic soil drought is characteristic of the Great Plains grassland (Clements and Weaver, 1924; Albertson and Weaver, 1946). Available soil moisture has been found to be continuously absent from the second foot of soil for more than three years during drought and for periods of two months from the upper foot (Albertson and Weaver, 1942). Because of the occurrence of much of the precipitation in light showers, during which evaporation loss is high, and as heavy rains, when loss by runoff is high, the effectiveness of precipitation in replennishing soil moisture is variable (Campbell, 1936); Albertson and Weaver, 1942; Doughty *et al.*, 1943).

Plant cover is both a favorable and unfavorable factor in increasing the supply of moisture in the soil. Both living grass and associated litter increase the rate of infiltration of water into the soil and reduce runoff (Duley, 1939; Duley and Kelly, 1941). In this respect it is more significant than the type of soil (Duley and Domingo, 1949). However, the higher loss of moisture by evaporation of intercepted rainfall before it reaches the soil must be taken into account (Clark, 1940). A closer relationship has been reported between precipitation and available soil moisture in native grassland than in cropland (Flory, 1936).

The loss of soil moisture resulting from the growth of plants has been measured in several instances. The water loss from native grassland has been reported to be approximately one pound per square foot per day during active growth (Weaver and Crist, 1924) but increased to eight to 14 pounds in one study during drought (Weaver and Albertson, 1956). Losses from cropland have been as much as 2.5 times greater than from prairie (Weaver and Crist, 1924; Noll, 1939), while there is some evidence that under graz-

ing water loss from grassland is reduced (R. J. Weaver, 1941). The loss of water from a stand of dead grasses has been reported to be one-third and of a bare soil one-half that of normal prairie (Weaver and Crist, 1924). Great variations occur in the water requirements of different species in relation to the amount of dry matter produced, in some instances prairie species being more demanding in this respect than crop plants (Noll, 1939).

Variation in height of the water table has been considered to have no influence on the supply of soil moisture in upland prairie where it is usually many feet below the surface. However, in lowland a drop of three to four feet may occur in drought, causing severe damage to vegetation (Albertson and Weaver, 1945). Contour dykes have been found to be of substantial value in increasing soil moisture by reducing runoff (Hubbard and Smoliak, 1953).

While most writers have been concerned with periods of low precipitation in the Great Plains, periods of good rainfall have occurred between droughts throughout the Plains (Henry, 1931; Clements and Chaney, 1937). Savage (1937) regarded high temperatures as the climatic factor most damaging to plant growth in the central and southern Plains, as indicated by high plant mortalities in localities where precipitation was not much below normal. However, in the north low precipitation is probably most important (Sarvis, 1941).

Temperature

Mean temperatures are higher in periods of drought. The average daily maximum temperatures at Hays, Kansas, for June, July and August were 8.0°, 7.5° and 4.4°F. higher, respectively, during four of the driest years of the 1930's than during the eight years preceding the drought (Albertson and Weaver, 1942). Similar data are recorded for South Dakota during a less severe drought in the same period (Black and Clark, 1942). Weekly means were sometimes 15°F. above normal (Albertson and Weaver, 1945). However, during a five-year period of above-average moisture in the northern Mixed Prairie the average mean maximum temperature during April to September was 5.4°F. below the long-term mean (Coupland, 1958).

High air temperatures during drought are associated with the higher temperatures in the soil which result from less protective

vegetative cover. The temperature of bare soil sometimes reaches 140° to 150°F. (Albertson, 1937; Weaver and Albertson, 1956). Air and surface soil temperatures are often higher in cropped land than in prairie (Flory, 1936; Noll, 1939).

Evaporation

That evaporation is markedly affected by variations in other weather factors is shown by data from two widely separated stations. During drought in 1934 seasonal evaporation from a free water surface at Hays, Kansas, was 34 per cent above the long-term average (Weaver and Albertson, 1942), while at Swift Current, Saskatchewan, it averaged 16 per cent below the long-term mean during a five-year period of moist weather (Coupland, 1958).

Wind

Wind movement is higher in dry years (Albertson and Weaver, 1942). This, together with combined effects of cultivation, overgrazing and drought, has created conditions extremely conducive to wind erosion and dust storms. "Black blizzards" were particularly well developed in the spring of 1935 in the central and southern Great Plains, and resulted in deposition of soil in drifts 2.5 feet high in many prairies and a thin layer one-half to one inch in depth over an extensive region (Albertson and Weaver, 1942). Cultivated land is subject to erosion by wind during the spring (windiest time) of most years, and only by progressive farming practices is frequent dusting prevented. Dust storms in the Great Plains occurred long before the 1930's (Malin, 1946; Tannehill, 1947), and they have developed since (Dale, 1947; Finnell, 1948), particularly from 1954 to 1956.

The relative humidity is often as low as ten per cent or less during drought (Weaver and Albertson, 1956), thus causing the wind to be more desiccating.

EFFECTS ON VEGETATION

Observations of the vegetation of the Great Plains during the nineteenth century indicated that the character of the grassland responds markedly to changes in weather conditions. Unfavorable reports of the agricultural potentialities of the region were made as a result of explorations during dry periods, so that the area

was designated by geographers as the "Great American Desert" for half a century (Webb, 1931), whereas traverses in periods of sufficient moisture prompted accounts of the fertility of the land and its suitability for settlement. Early reports on the vegetation were limited to its general condition in certain areas at a specific time and did not provide a measure of the degree of change in the same area over a period of years. Also, the characteristics of the vegetation referred to were few. Only during the last three decades have measurements of change been made involving density, floristic composition and yield. Most records deal with the effect of the drought of the 1930's, but some data gathered during drought in the 1950's support these findings. Studies in the 1940's recorded the nature of recovery of grasslands from drought, and recent work in one area provides a measure of response to an extended period of above-average moisture supply.

Forage Yield and Grazing Capacity

An early response of grassland to drought is reduction in forage yield (Weaver and Albertson, 1944), which is associated particularly with the effect of diminished precipitation in reducing soil moisture. Yield is closely related to the supply of soil moisture (Weaver and Crist, 1924; Hopkins *et al.*, 1952). The highest correlation between yield and a weather factor in the same growing season has been found to be with May plus June precipitation in the northern Mixed Prairie (Sarvis, 1941; Smoliak, 1956), while yield was negatively correlated with seasonal mean temperature, hours of bright sunlight and wind mileage (Smoliak, 1956). Forage yield has also been found to be closely related to the ratio of precipitation to evaporation (Clarke *et al.*, 1943). The relationship between amount of precipitation and production of native forage is not entirely the same as for the production of field crops, since the native vegetation has a longer growing season, is more deeply rooted, and exhausts soil moisture more (Sarvis, 1941).

Yielding capacity is a reflection of plant vigor. The immediate response to decreased moisture supply is a curtailment in height of growth. Only during prolonged drought does the density of the cover decrease, further reducing yield. Accordingly, unless drought has been very severe and prolonged, reduction in height is the main indication of poor growing conditions. The degree to which

height may be affected is indicated by data from western North Dakota (Whitman *et al.*, 1943). Here, drought in 1934 caused a reduction in leaf height of the major grass species of about one-third from that of 1933. After slightly higher growth in 1935, the height growth in 1936 was only one-fifth of that of 1933. Not until 1940 (four years after drought) was recovery in leaf height fully realized. Similarly in southeastern Montana (Campbell, 1936), *Agropyron smithii*[1] averaged 13 inches high in 1933, one inch in 1934, and 15 inches in 1935, while in west-central Kansas the short grasses remained dormant most of the summer of 1939 but grew to a height of three inches after late summer showers (Weaver and Albertson, 1940). Because of this great variability in vigor of drought-stricken vegetation and differences in degree of burial by dust, there is only a general correlation between basal cover and yield (Albertson and Weaver, 1944; Albertson *et al.*, 1957).

During drought forage yield declines sharply. Variations in the yield of mixed grasses in eastern Montana from 1,586 pounds per acre in 1927 to 222 pounds in 1934 have been reported (Campbell, 1936), while in southeastern Alberta the range was from 90 to 825 pounds per acre over a 24-year period (Smoliak, 1956). These fluctuations are similar in magnitude to those reported in west-central Kansas (438 to 2,951 pounds per acre) (Albertson *et al.*, 1957). Yield suffers most from drought when the grassland is being overused by livestock. Thus in western Kansas forage production in overgrazed pastures was reduced during drought to less than ten per cent of that in well-managed ones (Albertson and Weaver, 1942).

Reductions in forage yield are reflected in decreased grazing capacity of range. In western Kansas, where ten to 12 acres of range was required per animal unit before drought, 30 to 50 acres were needed at the end of the drought (Albertson and Weaver, 1942). To the northward in southeastern Montana the carrying capacity in the drought year of 1934 was only 36 per cent of 1933 and in 1936 was further reduced to 23 per cent (Hurtt, 1951), while in southeastern Alberta 70 acres were required in 1936 to produce the same amount of feed as was produced on 12 acres in 1942 (Smoliak and Peters, 1952).

[1] Botanical nomenclature in this paper is according to Hitchcock and Chase (1950) for the grasses and Fernald (1950) for other groups.

The reduced abundance of foliage has been reported to accentuate drought by reducing shade and providing less debris to protect the soil. Not only is leaf growth reduced and stopped unusually early during dry years, but blossoming and production of seed is often prevented (Weaver and Albertson, 1943). In western North Dakota the production of seed stalks was reduced to zero or a trace in 1934 and 1936 for all of the dominant and associated grasses, but by 1938 they were again produced in normal numbers by many species (Whitman *et al.*, 1943). Those few which were produced in dry years were reduced in stature, but to a less degree than leaf height.

Forage removal by grasshoppers is considerable during drought. On the grazed ranges of western North Dakota in 1936 an estimated 30 to 40 per cent of the current growth was removed by these pests (Whitman *et al.*, 1943).

Drought affects the vigor of plants below the soil surface as well as above it. Studies in western Kansas (Weaver and Albertson, 1943) have shown that during drought the root systems of the short-grass dominants were mostly restricted to the upper foot of soil, and below two feet roots were extremely scarce, although before the drought these species had rooted to depths of four to five feet. The root systems of forbs were likewise reduced, so that species which penetrated to depths of nine to 12 feet (*Sphaeralcea coccinea*, *Psoralea tenuiflora* and *Kuhnia glutinosa*) with normal soil moisture, were developed only to from four to six feet by the end of the drought of the 1930's. There is some evidence to indicate that with the beginning of this drought some species increased in depth of rooting, but as drought progressed and available moisture was limited to that from current precipitation, plants became dependent on moisture near the surface and deep roots were of no advantage (Weaver and Albertson, 1939, 1943).

During recovery of the grassland from the effects of drought, yield increases rapidly. This is true even of severely depleted ranges, when *Buchloë dactyloides* is an important component. In an overgrazed range in west-central Kansas, where the basal cover was reduced to two per cent and the yield to 133 pounds per acre in 1940 after seven years of drought, two years of good rainfall permitted an increase in cover to 31 per cent and in grass yield to 2,512 pounds. Yield increases were less abrupt in moderately

grazed areas (538 to 1,650 pounds) and in areas of postclimax tall-grass communities (1,825 to 4,379 pounds) which had not been depleted so severely in cover. The yield of weeds sometimes exceeded that of grasses during the first and second year of good rainfall, occasionally exceeding one ton per acre (Weaver and Albertson, 1944). These findings agree with those in the Edwards Plateau of Texas where the maximum response of grazed vegetation to rainfall is not immediate but requires a delay of one or two years, the vegetation response following years of low rainfall being slower than the response to years of high rainfall (Thomas and Young, 1954).

Rapid recovery of the range after drought was favored by the decline in livestock population made necessary by poor forage production during drought. As a result, ranges in Mixed Prairie were not fully stocked in the early years following drought (Whitman *et al.*, 1943), and the renewed plant cover increased more rapidly than the stock. In some areas "the ranges would probably have increased their perennial cover even more rapidly if moderate grazing had been generally employed and much of the foliage which later formed excess debris had been consumed or trampled to the ground" (Weaver and Albertson, 1944).

When prolonged drought causes loss of basal cover, response to increased availability of moisture is first expressed in increased height of grasses. This also occurs during the less unfavorable years of a long drought (Albertson, 1937). Weaver (1950) found that, in True Prairie sites near the transition of Mixed Prairie, height of grasses during the years immediately following drought was higher than during normal years because they were "freed temporarily from the community rule of severe competition".

When above-average moisture conditions prevail for an extended period of time so that development towards a postclimax type of vegetation is possible, yield increases occur above those of the climax. Accordingly, in 1955-56 the calculated yield of a large section of the northern Mixed Prairie was 237 per cent as great as in 1944, even though the vegetation in that region had been considered to have fully recovered from drought by 1944 (Coupland, 1958). However, above-average (20 per cent) precipitation after 1949 favored the change to a more productive community.

Density

The proportion of the soil surface which is occupied by the bases of plants (basal cover) in Mixed Prairie during periods of average weather ranges from less than ten per cent in mid-grass communities of *Stipa* and *Agropyron* (Tolstead, 1941; Coupland, 1950) to 85 per cent or more in areas where a disclimax turf of short grasses has developed from overgrazing (Albertson, 1937; Savage, 1937).

Arrival of drought rarely results in death of all plants. The first stage of degeneraton is marked by wilting of the least drought-resistant species which are not equipped for withstanding deficiency of soil moisture. If drought continues, these plants die. More drought-hardy species resist wilting and conserve moisture loss by rolling of leaves and assuming a condition of drought dormancy for periods of as much as several weeks at a time. Dormancy may alternate with growth several times in one season with species that can resist long periods without available soil moisture. *Bouteloua gracilis* and *Buchloë dactyloides* have a remarkable ability to recover rapidly from drought dormancy and make renewed growth. However, even the most xeric species decrease in numbers during intense drought, while the mesic ones disappear completely. Short grasses of tablelands were the first to manifest the effects of drought in the 1930's. In some instances the deeper-rooted species, for example, *Andropogon gerardi*, are able to survive far into drought because of their ability to reach soil moisture which is unavailable to shallower-rooted, but otherwise more xeric, species. During drought the straw color indicating dormancy appears frequently, but in 1934 and 1939 much of the vegetation became bluish-gray, a color indicative of death (Weaver *et al.*, 1935; Albertson, 1937; Weaver and Albertson, 1939, 1940a; Albertson and Weaver, 1942).

The death of some plants and decrease in vigor of others result in a reduction in basal cover of the vegetation. In this selective process many of the less xeric species of grasses and forbs are killed, and these species survive as dwarfed relicts only in the most favored locations. Among the most drought-resistant grasses the younger, more poorly rooted individuals succumb together with the less vigorous of the older plants.

The extensive studies of Weaver and Albertson in western Kansas have shown that losses of basal cover resulting from drought of 50 to 85 per cent were general. In the ungrazed *Bouteloua-Buchloë* community near Hays, Kansas, the original basal cover of 89 per cent decreased from 1934 to 1939 to the following percentages: 85, 66, 58, 25, 31 and 22, respectively. In the *Andropogon scoparius* community the total basal area of the vegetation decreased by 60 per cent. In the ecotone between the two communities small decrease in basal cover occurred because of the ability of the short grasses to take over from the mid grasses (Albertson and Weaver, 1942). Destruction of the grassland was so general that by the late 1930's the basal cover was five per cent or less in 40 per cent of the ranges studied in Mixed Prairie from Oklahoma to South Dakota (Weaver and Albertson, 1940a).

Reports are similar from other parts of the Great Plains. In western North Dakota the density of the plant cover in grassland decreased from 30 per cent to 13 per cent from 1933 to 1936 (Sarvis, 1941; Whitman *et al.*, 1943). There was rapid improvement of the cover in this area after 1936 because of cessation of drought and reduction of grazing pressure. In southeastern Montana the drought was most severe in 1934 when summer rainfall was only 37.9 per cent of average. Decreases in cover, ranging from 62 to 79 per cent, were recorded from 1933 to 1935 for the various dominant species (Ellison and Woodfolk, 1937), while a later report (Hurtt, 1951) showed reductions of 88 to 98 per cent in the density of various dominant species from 1933 to 1937 under moderate rates of grazing. Sharp declines were also measured in ungrazed areas. In the Mixed Prairie of southeastern Alberta records of fluctuations in density of vegetation caused by drought have been limited to those of Clarke *et al.* (1943). Here below-average precipitation occurred in 1931, 1934 to 1937, and in 1939. In the ungrazed *Bouteloua-Stipa* community basal cover of grasses decreased from 26 per cent in 1929 to 21 per cent in 1936. Drought then effected a rapid decline to 14 per cent in 1939. Albertson and Weaver (1942) have found that losses in basal cover are less severe in lowland areas of postclimax grassland.

Decrease in density is most rapid in early years of drought (Albertson and Weaver, 1942). Over a large area of the southern and central Great Plains decline in cover was estimated to be from 25

to 90 per cent during the first two years (1933-34) of the great drought (Savage, 1937). During prolonged dry weather a subsequent increase in cover sometimes results because of occupation of vacated areas by a more drought-resistant species (Albertson and Weaver, 1942).

Losses in basal cover are proportionally greatest in densely grassed areas unless these are dominated by the xeric, short grasses capable of rapid stolon production during short periods of moist weather (Weaver and Albertson, 1936). In the more open, ungrazed *Andropogon scoparius* grassland, where pre-drought cover was often only 25 per cent, the lowest cover reached during drought was 12 per cent (Albertson and Weaver, 1942).

Moderate grazing, while intensifying to some extent the unfavorable effects of drought, seems to be a factor of less importance than climate in modifying the plant cover. However, the influence of heavy grazing is of as great or greater importance than that of climate. Losses in basal cover are sometimes less in moderately grazed pastures than in ungrazed prairie. This has been attributed to the previous effect of grazing in favoring drought-resistant species (Weaver and Albertson, 1936), especially *Buchloë* which proportionally increases in cover under close clipping because of reduced competition from taller grasses (Savage, 1937). In west-central Kansas, where losses in ungrazed prairie were 85 per cent by 1936, the loss nearby under moderate grazing was 72 per cent. In south-central Kansas the respective losses were 60 and 36 per cent, and in north-central Kansas 50 and 54 per cent: "Excessive growth of the vegetation during good years preceding the drought made it more susceptible to drought injury than pastures which had been moderately grazed". This advantage of formerly moderately grazed areas was evident particularly where grazing was discontinued during drought. In other short-grass ranges the degree of damage was lowest in ungrazed prairies, and maximum reduction in cover occurred a year later than under grazing (Albertson and Weaver, 1942). Under heavy grazing, however, loss in density was greatest, being 91, 74 and 91 per cent, respectively, in the west-, south- and north-central Kansas (Weaver and Albertson, 1936; Albertson and Weaver, 1942). These findings agree with those of Savage and others (Savage and Jacobson, 1935; Savage, 1937) in the same area, of studies in the northern Great Plains (Clarke

et al., 1943), and the general observations of (Campbell, 1936) that the worst depletion that has occurred during all droughts was in overgrazed ranges.

Under certain conditions basal cover may increase during drought after the first losses have been experienced. In overgrazed areas of *Andropogon scoparius* vegetation in west-central Kansas the basal cover was reduced to 11.5 per cent by 1935 and to 9.3 per cent in 1936, when *Bouteloua curtipendula and B. gracilis* made up half of the cover. By 1939 the cover had again increased to 30 per cent and included *Buchloë* as a prominent constituent. *Andropogon scoparius* had practically disappeared. In the transition area in western Kansas, between the short grass and *Andropogon scoparius* types, the cover was reduced from 65 to 25 per cent and then increased to 50 per cent by 1939 because of increases of short grasses and entrance of *Bouteloua curtipendula*. (Albertson and Weaver, 1942).

The native forbs suffer great reductions in drought as well as the grasses. The nature of these losses is variable. Some die with the first impact of drought, while others suffer midsummer drought above ground, only to regrow the following spring. Wilting, drying and defoliation of tops by grasshoppers are other common phenomena. The most drought-resistant species are affected principally by reduction in stature. Reduction in numbers of stems, death by mechanical injury from blowing dust, and smothering by a blanket of dust were other common effects of drought. Of the 28 most abundant forbs of Mixed Prairie in the central Great Plains, three species (*Lomatium*) persisted in normal numbers at the end of the drought of the 1930's, 14 disappeared and 11 lost heavily (Weaver and Albertson, 1943). *Sphaeralcea coccinea* was the only generally distributed native, non-grassy species, aside from cactus, that increased in Mixed Prairie (Weaver and Albertson, 1944). Vegetative reproduction made a manifold increase possible. Early growth in spring and its habit of semi-dormancy during drought enabled it to endure. A group of forbs which suffered great losses but were never exterminated included *Psoralea tenuiflora, Haplopappus spinulosus, Lygodesmia juncea, Cirsium undulatum, Gaura coccinea, Solidago mollis, Kuhnia glutinosa, Mirabilis linearis* and *Liatris punctata*. By 1939 in Mixed Prairie from Oklahoma to South Dakota many of the less xeric forbs had practically disap-

peared, only six or eight of the most xeric native ones being regularly represented by much dwarfed and widely-spaced individuals (Weaver and Albertson, 1940a). The number of stems was reduced in 1940 to an average of about 500 per acre in 14 sites in western Kansas, where only eight native species of forbs were encountered in sampling, the number averaging five per station (Weaver and Albertson, 1943). In the driest area the xeric short grasses were almost the only species surviving, and these were greatly reduced in area, so that *Bouteloua gracilis* and *Buchloë dactyloides* were the chief grasses of western Kansas prairies in 1939 (Weaver and Albertson, 1940; Albertson and Weaver, 1942). The abundance of *Sphaeralcea coccinea* and the paucity of most other forbs was noted in 1957 by the present writer during a tour of the drought area of the southern Great Plains, thus suggesting the similarity of effects of both recent droughts on this component of the vegetation.

In western North Dakota perennial forbs maintained themselves through the less severe drought period and increased after the driest years (Whitman *et al.*, 1943).

A portion of the soil surface vacated by grasses provided a chance for certain forbs which increased during drought. Throughout Mixed Prairie from Oklahoma to South Dakota certain species of cactus (mostly *Opuntia* spp.) increased so greatly in abundance that they constituted a serious weed problem by 1939 (Weaver and Albertson, 1940a). They became so thick that sometimes it was impossible for cattle to lie down without contacting the spines, and native species were frequently protected from grazing by their presence. Their spread was possible because of the remarkable adaptability of the plants to increase in size by rhizome development, the wide distribution of seed and vegetative parts by rodents and cattle (Harvey, 1936; Costello, 1941; Turner and Costello, 1942; Weaver and Albertson, 1944), and the decrease in numbers of parasitic insects associated with the dry conditions (Cook, 1942). Ruderal species, while not necessarily increasing in abundance, are most numerous in grassland depleted in cover by drought (Savage, 1937) or other means.

The losses in density of vegetation experienced in Mixed Prairie were less pronounced in True Prairie. However, deterioration of grassland due to drought was common west of the Missouri River

and increased in degree westward to the edge of the Mixed Prairie. By 1939 the basal cover of depleted *Andropogon scoparius* prairies in eastern Nebraska was generally one-half to two-thirds of normal. Where *Agropyron smithii* had replaced *Andropogon*, there was sparse growth which permitted an open pattern of bare soil. Farther eastward in southeastern Iowa the prairies had not suffered deterioration by 1939 (Weaver and Albertson, 1936, 1939, 1940).

One of the most important indirect effects of drought on the grassland was the widespread deposition of dust in depths ranging from a thin film to drifts two or three feet deep, a layer from one-half to two inches in depth being common. This frequently accentuated the damage caused to vegetation by the scarcity of soil moisture (Albertson and Weaver, 1942, 1944; Lacey, 1942). However, a light cover of dust has sometimes furnished some protection against drought by aiding dormancy of grasses (Albertson and Weaver, 1944).

Not sufficient attention has been given to the modifying influence of slope exposure with respect to reaction of vegetation to drought. In True Prairie in eastern Nebraska perennial grasses suffered less from drought on mesic slopes than on xeric ones or on level ground (Robertson, 1939).

After favorable periods in drought, myriads of grass seedlings sometimes appear in the open spaces between living bunches, but nearly all succumb. Despite quantities of seedlings and rapid propagation of *Buchloë* by stolons in 1935 and at other times during the drought of the 1930's, periods favoring growth were too short to result in establishment (Albertson and Weaver, 1942).

Recovery of vegetation from severe damage during drought is accomplished through secondary succession (a subsere) towards the climax. In the central Great Plains two types of succession were differentiated, depending on the degree of depletion (Weaver and Albertson, 1944). Succession on badly or completely denuded range was through a first weed stage comprised of annuals, a second weed stage of weedy grasses and some perennial forbs, an early native grass stage in which *Agropyron smithii* and *Sporobolus cryptandrus* were conspicously represented, and a late grass stage in which the other native species were approaching their previous degrees of abundance. In ranges reduced to one-fourth or more of normal cover but with sufficient perennial grasses to re-

generate quickly, the abundance of annual forbs was diminished, resulting in only one weed stage. In both seres, *Salsola kali* var. *tenuifolia* and *Erigeron canadensis* were important pioneers.

Weaver and Mueller (1942) found the number of seeds of native grasses and forbs to be few after drought and concluded that several years of good seed production and development of seedlings into mature grasses are necessary for the restoration of mid-western ranges. An average of 73 seedlings occurred per square foot in soil samples collected in 1941 from a large section of Mixed Prairie in western Kansas and eastern Colorado and grown in the greenhouse, about 40 of these being grasses. Seventy-five per cent of the latter were *Sporobolus cryptandrus* (26 per square foot), *Bouteloua gracilis* (3.7) and *Buchloë dactyloides* (0.5). Due to heavy mortality in the native habitat, however, the numbers there were smaller, averaging 2.4 perennial grass seedlings per square foot in the most favored part of western Kansas. In 1942 conditions for germination and survival coincided, resulting in a heavier stand of seedlings (Weaver and Albertson, 1944). In addition to seeding, other methods of recovery of grasses include increases in the size of relicts by tillering, production of rhizomes and stolons, and breaking of dormancy in old root crowns and underground parts (Weaver and Albertson, 1944). In the central Great Plains after the drought of the 1930's, breaking of dormancy usually occurred in the first three years of adequate rainfall, sometimes after the plants had been dormant for five to seven years. Seedlings of forbs grew well after one or two years of good precipitation, some seeds having been dormant for seven years. Recovery of forbs from dormant vegetative parts was also common.

The rate of recovery from drought varies widely, depending on the kind of pre-drought cover, degree of depletion, kind of grass relicts surviving, amount of damage from burial by dust, intensity of grazing and trampling during recovery, and amount and distribution of local precipitation (Weaver and Albertson, 1944).

More rapid recovery is possible where *Buchloë dactyloides* comprises a prominent part of the vegetation, thus permitting stoloniferous spread. In western Kansas a short-grass cover of 13 per cent in 1940 increased to 48 per cent by 1942 and to 72 per cent by 1944 (Albertson and Weaver, 1946). In another instance an ungrazed pre-drought short-grass cover of 89 per cent which had

been reduced to 20 per cent by 1940, again increased to 90 per cent after three years of recovery. Recovery was always slower where *Bouteloua gracilis* alone remained than where *Buchloë* was present. Near Tirbune, Kansas, the cover of *Bouteloua* increased from five per cent in 1940 to 13, 18 and 21 per cent in the three succeeding years, while the only other grass species of importance increased from a trace to six per cent. In another range nearby the increase in cover of *Bouteloua* was from two to 15 per cent during the same period. In contrast, in a pasture near Kendall, Kansas, *Buchloë* increased in cover from two to 34 to 47 per cent from 1941 to 1943, while *Bouteloua* and *Sporobolus cryptandrus* each increased only from one to three per cent. Similarly, in a range near Marienthal, Kansas, *Buchloë* increased in basal cover from 1940 to 1943 as follows: two, 24, 84 and 93 per cent, while *Bouteloua* increased from one to five per cent (Weaver and Albertson, 1944).

Moderate grazing was no great handicap in recovery of short-grass vegetation from drought. Increases in *Buchloë* were made following drought, even under heavy grazing. Thus, near Quinter, Kansas, Weaver and Albertson (1944) report that *Buchloë* increased in basal cover from four per cent in 1940 to 12, 47 and 79 per cent, respectively, in the next three years, while the cover of *Bouteloua* was four, 12, 28 and 16 per cent, respectively. These increases were similar to those recorded near Hays in a stand which had been under protection from grazing since 1932. Here the increases during the same period were from nine to 66 per cent for *Buchloë* and from ten to 22 per cent for *Bouteloua*. In another overgrazed pasture a short-grass cover of three per cent in 1940 increased to 93 per cent in 1943.

The combined effects of dusting and overgrazing slowed down recovery so that where these had reduced the cover to two per cent by 1940, the effects were still seen in a 26 per cent cover in 1943, while under light dusting and moderate grazing use the density of the vegetation had increased to 76 per cent. The amount of relict vegetation largely determined the rate of recovery on ranges with drifted soil. While occasionally it was rapid, usually annual weeds persisted in abundance (Albertson and Weaver, 1944).

Bouteloua curtipendula played a prominent role in recovery of the postclimax *Andropogon scoparius* community in west-central

Kansas (Weaver and Albertson, 1944). In a closed type of community (where the total basal cover was 60 per cent before drought) *Bouteloua curtipendula* increased in basal cover from seven to 27 per cent from 1940 to 1943, while in an open type (formerly of 25 per cent basal cover), this species underwent a similar increase (from 9 to 22 per cent). Drought had caused conversion of the postclimax *Andropogon* community to one of mixed prairie.

On sandy loam soils *Sporobolus cryptandrus* frequently played an important part in recovery, as near Quinter, Kansas, where it increased in a range from one-half per cent basal cover in 1940 to 12 per cent in 1943, while *Bouteloua gracilis* and *Buchloë* increased from 1.6 to 18 per cent and from one to 32 per cent, respectively (Weaver and Albertson, 1944).

Recovery from the drought of the 1930's was delayed somewhat in the southwestern Great Plains by the occurrence of midsummer drought in 1943. In this "dust bowl", where perennial grasses were very sparse as a result of drought, recovery of vegetation was often the result of seed dispersal, even with species like *Buchloë dactyloides* in which vegetative reproduction is rapid (Weaver and Albertson, 1944).

Following periods of good rainfall, forbs began to increase in numbers as well as stature. This increase was from rhizomes (*Solidago mollis* and *Cirsium undulatum*), from seed from relict plants (*Haplopappus spinulosus*), and perhaps more frequently from seed which had lain dormant since before the drought (*Psoralea tenuiflora*). The openings in the sod became populated. *Ratibida columnifera* was particularly common. *Gutierrezia sarothrae* was another forb which disappeared early in drought and returned promptly after its cessation. Many forbs were first observed after drought on north hillsides, in depressions and in other favorable refuges (Weaver and Albertson, 1944).

The abundance of weedy grasses and forbs, which occupied bared areas within the thinned cover of perennials during the first year or two of favorable weather, soon decreased. But the return of native forbs was slow. Their paucity in 1943 is indicated by these data. In 19 ranges in western Kansas and eastern Colorado, the average number of species present was 16 (ranging from five to 28), five per cent were very abundant, and four, 11, 20 and 60

per cent ranked, respectively, as abundant, common, infrequent and rare (Weaver and Albertson, 1944).

Of 44 chief species of Mixed Prairie, only five showed marked recovery by 1943 (*Ambrosia psilostachya, Gutierrezia sarothrae, Ratibida columnifera, Psoralea tenuiflora, Haplopappus spinulosus*), 27 showed partial recovery (including *Astragalus* spp., *Cirsium undulatum, Gaura coccinea, Grindelia squarrosa, Liatris punctata, Oxytropis lambertii, Penstemon albidus, Senecio plattensis* and *Solidago missouriensis*) and 12 showed no recovery (including *Antennaria campestris, Aster multiflorus, Erysimum asperum, Lithospermum incisum, Lygodesmia juncea* and *Psoralea esculenta*) (Weaver and Albertson, 1944).

After drought *Sphaeralcea coccinea* decreased in numbers, nearly regaining its pre-drought abundance (Weaver and Albertson, 1944).

Cactus (mostly *Opuntia* spp.), which had become very abundant in drought, decreased rapidly in the first four years with more than normal precipitation. Its increase during drought was primarily due to the reduced competition from the depleted plant cover but also to the aridity of the atmosphere which was unfavorable to the development of insect parasites (Weaver and Albertson, 1944; Costello, 1941; Cook, 1942).

With continued favorable weather in the 1940's the cover continued to improve so that in even the most denuded areas it was similar to the pre-drought cover by 1950. Development of the vegetation was again interrupted by drought in the early 1950's. At Hays, Kansas, drought was more severe from 1952-54 than in any three-year period of the previous drought. A survey in 1955 and 1956 revealed losses from the pre-drought cover of 20 to 30 per cent in western Kansas, 29 to 67 per cent to the northward, northwestward and westward into adjacent States, and 30 to 41 per cent in parts of Oklahoma and the Texas panhandle. These losses were in ungrazed areas, those in grazed areas being much greater (Albertson *et al.*, 1957).

In the northern Mixed Prairie drought was not so severe in the 1930's and the cover was restored by 1944 (Coupland, 1950). Moreover, during the second decade following drought, moisture conditions were far above average, resulting in a further doubling of the basal cover (Coupland, 1958).

Floristic Composition

While changes in forage yield and density of plant cover are the most immediate and conspicuous responses of grassland to changes in weather, the botanist may find the fluctuations in the relative abundance of species more interesting. Early detailed records of variations in composition are not available. However, after a scrunity of reports on grassland in the Great Plains from 1889 to 1915 and of field notes made by himself from 1897 to 1918, Clements (1920) concluded that the mid grasses comprise a portion of the vegetation of the Mixed Prairie during periods of dry weather as well as moist. He stated that the mid grasses were as abundant and universal in the dry years, 1916-1918, as in the exceedingly wet year of 1915. The only evident response to drought was a marked reduction in height and in the number of flower-stocks, a reduction which affected *Bouteloua* as much as *Stipa*, though hardly as much as *Agropyron*.

During the drought of the 1930's the true extent of the fluctuations in composition of Mixed Prairie communities was ascertained for the first time by quantitative measurement within the same areas over a period of many years. These studies were most intensive in the central Great Plains, but sufficient records were made in other areas to provide an interpretation of the probable extent of fluctuations throughout the Mixed Prairie.

During drought a marked change occurred in the relative abundance of *Bouteloua gracilis* as compared to *Buchloë dactyloides* throughout the community dominated jointly by these grasses. In the short-grass type of west-central Kansas they had shared equal prominence before drought began in 1933. Due to the greater drought resistance of *Bouteloua*, it suffered less heavily during drought and by 1940 occupied 1.7 times the area of *Buchloë* (59 and 35 per cent of the basal cover, respectively). However, due to the remarkable ability of *Buchloë* to develop new stolons almost immediately following rain, it became dominant after drought to make up five-sixths of the vegetation in 1942. In the subsequent favorable years *Bouteloua* increased slowly in abundance at the expense of *Buchloë*, but not until 1951 did it again share equal prominence with *Buchloë* (Albertson and Weaver, 1942; Weaver and Albertson, 1944, 1956).

In communities comprised of both mid and short grasses before drought, the tendency was for elimination of the mid grasses during drought. The most detailed study in which a transformation of this type was recorded was that reported by Albertson and Weaver (1946) in north-central Kansas. Replacement of mid grasses by short grasses was accompanied by a reduction in the number of species of forbs by 70 per cent. A decade of favorable weather was not sufficient for the mid grasses to become well re-established. During 1939 Weaver and Albertson (1940a) conducted a regional survey in western Kansas and Nebraska and the four adjacent States to study the effects of drought in 88 representative ranges. They found the vegetation reduced to a short-grass community of sparse cover. This had resulted from overgrazing, grasshoppers, desiccation and dust deposit. Dust films of one-half to two inches in depth were usually found, a deposit of one inch being sufficient to kill much of the short-grass cover. Towards the northern part of the region *Carex stenophylla* var. *enervis*, *C. filifolia*, *Stipa comata* and *Agropyron smithii* were often intermixed with the short grasses. Elsewhere the mid-grass layer had usually completely disappeared, even where overgrazing had not been a factor. Many forbs had also practically vanished, while often only remnants of the most persistent forbs remained. Many annual species had occupied the bare soil resulting from destruction of the grass cover, but even these had succumbed by August of 1939. After the drought succession proceeded through weedy and short-lived grass stages towards the short-grass community (Weaver and Albertson, 1944). This was modified in some areas by regrowth from the formerly dormant crowns of other species.

Recovery from drought in western Kansas, eastern Colorado and western Nebraska was closely connected with the behavior of three species, the short grasses, *Buchloë dactyloides* and *Bouteloua gracilis*, and a mid grass, *Sporobolus cryptandrus*. *Buchloë* had greatly diminished in relative abundance from its equal pre-drought status with *Bouteloua*. It had entirely disappeared from some ranges and remained only in the more favorable habitats or as occasional tufts in others. *Bouteloua* is much more drought resistant and was never killed so uniformly or completely over a wide area. Surviving clumps often increased greatly in diameter during drought. *Sporobolus*, which, while widespread, was abundant only

in sandy soil before the drought, often occurred abundantly in drought. It spread widely by wind-blown seeds to occupy denuded soil (Weaver and Albertson, 1944).

In the postclimax mid-grass community of west-central Kansas, dominated by *Andropogon scoparius*, only ten to 20 per cent of the cover of this dominant species survived after two years of drought. Here moisture conditions were sufficiently favorable to permit the increase of climax species of Mixed Prairie, notably *Bouteloua curtipendula* and *B. gracilis*. Over extensive areas of level land *Andropogon scoparius* completely disappeared late in the drought. The deep root systems of *A. gerardi* permitted it to survive in some instances where the shorter-rooted species disappeared. Recovery from drought in the *Andropogon scoparius* type was associated with the continued importance of the short-grass and more xeric mid-grass invaders. *Bouteloua curtipendula*, once established in bared areas, spread consistently, mostly by short rhizomes, the young shoots from them surviving more severe drought than the seedlings. Plants of *B. gracilis* increased by tillering, the increase being very slow but constant (Albertson and Weaver, 1942). The character of the community was so modified by drought that the importance of *A. scoparius* declined from its position of making up five-sixths of the total grass cover in 1932 to four per cent of the cover in 1937, and *Bouteloua curtipendula* and *B. gracilis* increased from a position of insignificance in 1932 to make up, respectively, 60 and 30 per cent of the cover in 1939. Not until 1943 were clumps of *Andropogon scoparius* again observed throughout this grassland type. These were mostly new growth from crowns of plants which underwent deep dormancy during drought. A single decade was long enough for this species only to begin to re-establish its former communities (Weaver and Albertson, 1944).

These changes corresponded with those in similar communities of True Prairie where these species were prominent. During drought, species of Mixed Prairie invaded some of the land formerly occupied by the *Andropogon scoparius* community of True Prairie (Weaver and Albertson, 1939, 1940, 1944; Weaver, 1943, 1950). Drought-evading *Agropyron smithii* and drought-resisting *Bouteloua gracilis*, each of which formerly made up less than one per cent of the basal cover, were particularly notable in this respect,

and dominated, respectively, the second and fifth communities in order of extent in the True Prairie of eastern Nebraska in 1943. In some districts they grew in association to compose a mixed-prairie type, which was the most widespread of all vegetation types in the region. Prominent among the other grasses which invaded the *Andropogon* community were *Stipa spartea* and *Sporobolus heterolepis*, which formerly occupied drier hillsides in True Prairie, and *Buchloë dactyloides*, a xeric short grass of Mixed Prairie (Weaver *et al.*, 1940; Weaver and Darland, 1944; Weaver, 1950). *Sporobolus cryptandrus*, formerly rare in eastern Nebraska, also increased in pastures of True Prairie because of its early seasonal development, resistance to grazing and prolific seed-setting properties (Weaver and Hanson, 1939; Weaver and Bruner, 1945; Weaver, 1954). These changes in the western part of the True Prairie resulted in the production of Mixed Prairie communities by 1941. The transformation was more rapid when the native prairie had been weakened by grazing and trampling or where it had degenerated to short-grass pasture previous to drought. By 1948 pure stands of *Bouteloua* and *Agropyron* were less abundant because of reciprocal invasions of each species in areas previously dominated by the other. "This intermixing resulted not in the re-establishment of true prairie but of mixed prairie instead" (Weaver, 1950).

In other parts of the Mixed Prairie to the northward the modification of the composition of the vegetation was not so great because of less severe or shorter drought. Usually the mid grasses were not eliminated by drought alone, so that they were present to reoccupy denuded areas after the drought. In grazed Mixed Prairie of western North Dakota *Stipa comata* was severely damaged by drought to lose its position as a dominant, while *Agropyron smithii* increased from its scattered distribution to become the dominant mid grass (Sarvis, 1941). These changes were considered to be due largely to the effects of drought. In other studies in western North Dakota and southeastern Montana (Ellison and Woolfolk, 1937; Whitman *et al.*, 1943; Hurtt, 1951) *Bouteloua gracilis* (a short grass) declined in cover faster than the mid grasses. However, the species which evaded drought by early spring growth were able to increase during the same period, and by 1941 all major species had regained their former abundance. In southeastern Mon-

tana the effects of drought were very similar but more damaging than those reported in North Dakota. In southeastern Alberta (Clarke *et al.*, 1943) the cover of the major grasses (*Stipa comata* and *Bouteloua gracilis*) declined markedly, while that of the early-growing, short-seasoned grasses increased greatly. This far north death of plants was not general, even the mid-grass decreases being associated only with decreases in size of clumps.

Thus it is seen that during drought mid-grass communities were replaced by mixed-grass communities, mixed-grass communities became dominated by short grasses, and the species composition of short-grass communities, which had previously resulted from overgrazing, was modified. These changes were on such an extensive scale that they resulted in the migration of the Mixed Prairie eastward for a distance of 100 to 150 miles into an area climatically (on the average) capable of supporting True Prairie from eastern South Dakota to east-central Kansas (Weaver, 1943; Weaver and Bruner, 1954) and in Oklahoma (Carpenter, 1939). In the ecotone between the associations, Mixed Prairie spread downwards on the hillsides. Clements and Chaney (1937) have stated that the "supreme factor in control of life in the prairie has been drought . . . Westward over prairie and plain, aridity is cumulative and drought increases in frequence to correspond, but its effects upon the biome are most severe in the middle region, where it alternates sharply with adequate rainfall and hence where compensation for it is most difficult".

In considering the recovery from drought of a portion of the True Prairie west of the Missouri River and near the transition to Mixed Prairie, Weaver (1950) has found that repopulation of bared soil after drought is largely by a "tremendous increase in the most drought-evading and drought-resisting perennial species. Many changes in plant populations occurred subsequently. These included the increase of former dominants, then of small abundance; the suppression of drought dominants under the wetter phase of the climatic cycle; the disappearance or reduction to normal numbers of other relicts of drought populations; the increase of drought-depleted forb populations; and a new development of societies . . . The re-establishment of the understory in the vegetation and the building of a soil mulch would also mark the

return to pre-drought climax conditions". These methods and sequence of recovery from drought are also applicable to the Mixed Prairie (Weaver and Albertson, 1944).

In depressional areas the effects of the drought were not so severely felt. For example, *Andropogon gerardi* was able to survive in a dormant condition in its postclimax community which, by 1943, had practically recovered from drought (Weaver and Albertson, 1944).

That survival of native species in disturbed areas does not always follow the same trends as in undisturbed areas is indicated by a report from the southern Great Plains (Savage *et al.*, 1948) that naturally regrassed abandoned farm lands withstood the effects of drought from 1933 to 1936 much better than did the vegetation on adjacent range land which had never been plowed.

An extended period of above-average moisture conditions may result in the replacement of the usual mid-grass dominants of Mixed Prairie by more mesic mid-grass species. Coupland (1958) found that in the northern Mixed Prairie the vegetation on brown soils changed during the period from 1944 to 1956 so that the proportion of the basal cover occupied by *Stipa comata* and *Bouteloua gracilis* decreased from 62 per cent to 40 per cent, while that comprised by *Stipa spartea* var. *curtiseta* and *Agropyron* spp. increased from 15 per cent to 31 per cent.

ADAPTABILITY OF SPECIES

These fluctuations in yield, basal cover and floristic composition occur because of the differential response of various species to changes in habitat characteristics as affected by weather.

Shantz (1927) divided plants of dry areas subject to drought into four groups, those which: (*a*) escape drought by a short, rapid growth period; (*b*) evade drought by conserving the scanty moisture supply by small size, restricted growth, wide spacing and low water requirement; (*c*) endure drought by passing into a drought-dormant condition; (*d*) resist drought by storing up a supply of water in their bodies to be used when none can be secured from the soil and have the ability to push their roots in dry soil. They do not possess any superiority in their ability to make growth in a dry soil and often no greater efficiency in the use of water. True drought must be considered with regard to the plants

involved. Levitt (1951) has pointed out the basic similarity between heat, frost and drought resistance, and indicates the possibility that what is usually considered drought resistance may sometimes be heat resistance. The ability of some plants to increase osmotic pressure of cell sap in response to lowering of available soil moisture has been related to drought resistance (Stoddart, 1935).

Grasses are adapted in different ways to withstand the effects of drought and to recover from drought. The studies of Weaver and Albertson in Kansas have shown conclusively that, while *Bouteloua gracilis* is actually more drought resistant than *Buchloë dactyloides* and can therefore maintain its cover better during drought, the latter species is well adapted to recovering area following drought because of its remarkable ability to produce stolons, sometimes as rapidly as 2.25 inches per day (Mueller, 1941). Seedlings of *Bouteloua gracilis* have also been found to be more drought resistant than those of *Buchloë* (Mueller and Weaver, 1942). *Agropyron smithii* is a successful competitor for the meagre amount of soil moisture which is available at times during drought. Its ability to make early luxuriant growth when water becomes available characterizes its efficiency in this respect. Any reproduction which occurs from seed must also take place during favorable periods, since the seedlings are very sensitive to drought damage (Mueller and Weaver, 1942). Once present it is well fitted by rhizomes to increase the area occupied and will stand more burial by dust than other grasses (Mueller, 1941). The open stand of this species and the lack of debris under it reduce the protection afforded to the soil, thus resulting in poor percolation of moisture. The species is therefore able to withstand invasion by deeper-rooted species for extensive periods, even after drought (Weaver, 1942). Other species which evade drought by growth early in the season include *Koeleria cristata* and *Poa secunda* as well as some sedges, notably *Carex stenophylla* var. *enervis*. Sometimes this faculty permits them to increase while the climax dominants decrease (Ellison and Woolfolk, 1937; Clarke *et al.*, 1943; Whitman *et al.*, 1943; Hurtt, 1951). In years of summer drought only, the early crop of cool-season grasses provides most of the grazing for the remainder of the year (Allred, 1945). The deep rooting habit of some species, e.g. *Andropogon gerardi*, permits survival for

longer periods than with some of the shorter-rooted species, even though these have more capacity to resist desiccation (Albertson, 1937). On upland rooting depth may be greatly reduced during drought (Weaver and Albertson, 1943). This suggests that in drier locations survival of species may depend on their ability to develop an efficient absorbing root system in the upper foot or two of soil. On the other hand, the ability of more mesic species of mid grasses to dominate in place of more xeric ones during periods of above-average precipitation is undoubtedly associated with the ability of the former group to more fully utilize the habitat factors and to compete with the latter group by their greater vigor.

That the relative response of species to drought may vary in different parts of a region as large as the Great Plains is indicated by reports from western North Dakota and southeastern Montana that among the major species *Bouteloua gracilis* and *Agropyron smithii* were the most severely injured by drought and were the slowest to recover (Ellison and Woolfolk, 1937; Whitman *et al.*, 1943; Hurtt, 1951). Perhaps this could be explained by differential response of species under a shorter growing season and/or during a shorter drought period.

Perennial forbs constitute a normal part of the vegetation in the Great Plains grassland. These are not usually conspicuous except in abnormally wet seasons. However, in dry years practically all forbs are absent or inconspicuous (Savage *et al.*, 1948). Decreases during long periods of drought are not gradual but sporadic, corresponding with the severity of drought. Many shallow-rooted plants are sometimes nearly all killed the first year, while more deep-rooted ones persist for many years, some deep-rooted forbs not losing heavily until near the end of the drought (Weaver and Albertson, 1943). Despite the near extinction of some forbs during drought, many are well adapted for recovery from dormant underground parts, from dormant pre-drought seed and from seed from relict plants. The adaptability of several species of cactus to withstand drought is indicated by increases in their numbers. However, these gave way to less xeric grasses and forbs when better moisture conditions prevailed. Everywhere the tendency was finally to regain the approximate importance which each species had previously held. The speed of this succession was determined largely by the adaptability of the species involved. Where

reproductive structures of the native plant species were too sparse, the adaptable ruderals with short life cycles were able to occupy bared areas temporarily during the early stages of recovery.

The ability of various species to withstand desiccation has been measured in terms of osmotic pressure (Weaver *et al.*, 1935; Stoddart, 1935). During these studies *Poa pratensis*, *Koeleria cristata*, *Antennaria campestris* and other shallow-rooted species dried in May of 1934 after developing osmotic pressures of only 18 to 27 atmospheres. In forbs rooted more deeply than eight feet the effect of drought on the tissues was slight, while in shallow-rooted forbs the increase in osmotic pressures was eight to 38 atmospheres, resulting in wilting and drying of many species.

While only dwarf shrubs are ever frequent in climax Mixed Prairie, the woody habit is well represented by vigorous species in adjoining formations as well as in postclimax situations and overgrazed areas within the grassland zone. Accordingly, the distribution of these shrubs fluctuates with varying weather in the grassland, depending on their ability to respond. Many shrubs extend by means of rhizomes into grassland (Weaver and Kramer, 1932). Invasion of these is favored by moist cycles and reversed by dry ones along the moist edge of the grassland (Clements *et al.*, 1929), while the reverse occurs with regard to the xeric shrubs (such as *Prosopis*) along the dry edge of grassland when the grass cover is thinned (Thomas and Young, 1954). With favorable weather and grazing conditions climax grasses can again displace such invaders (Cooper, 1953).

The woody species of postclimax situations within the grassland and in adjacent forest borders have a tendency to invade grassland during moist periods. This advance in a dry climate is possible because of small size, usually wide spacing and very extensive root system of such species as *Quercus macrocarpa* which competes successfully against grasses and shrubs because of rapid growth and deep penetration of its young roots and by their widely spreading habits (Weaver and Kramer, 1932). However, because of their long life cycles they cannot invade far before they are eliminated by drought (Coupland, 1958). Even in planted shelterbelts general killing occurs of trees which have become well established during a previous extended period without severe drought (Schulz, 1935), 73 per cent mortality occurring in some

districts (Deters and Schmitz, 1936). When native species are transplanted among shrubs, they may survive better than among grasses, since shrub invasion is the forerunner of trees (Clements *et al.*, 1929). More than 50 per cent of the trees died during the drought of the 1930's in almost all parts of the Mixed Prairie region. Often they survived longer in slightly drier sites, such as the top of a slope, than in moister ones because of better developed root systems (Albertson and Weaver, 1945). While most writers agree that intermittent drought is the principal factor in preventing invasion of the Great Plains grassland by trees (Clements *et al.*, 1929), some consider fire to be more important (Sauer, 1950; Stewart, 1953).

SUMMARY AND CONCLUSIONS

The Mixed Prairie grassland of the Great Plains of North America is subject to great fluctuations in weather. When drought is of sufficient duration to cause the death of native species by desiccation, a considerable modification in the floristic composition of the vegetation results. Some species are able to survive by going into drought dormancy. Reduction in basal cover, height, forage yield and seed production are characteristic of species undergoing drought conditions, even of short duration, while depth of rooting is reduced during dry periods of longer duration. Some species are adapted in varying degrees to endure or escape drought by their deep-rooting habit, their short-growing period in the cool part of the year, the ability of their tissues to withstand desiccation (associated with the ability to increase osmotic pressure markedly), and their ability to assume drought dormancy. Some species are able to overcome the effects of drought more rapidly than others. Notable among these is stoloniferous *Buchloë dactyloides* which is able to re-occupy denuded areas between plants during the first two years following a major drought.

Effects of drought are not limited to those of desiccation Where layers of dust are deposited, moisture penetration may be so affected that the habitat is transformed and occupied by other species, particularly *Agropyron smithii*. Drought is also often accompanied by hordes of grasshoppers which accentuate an already serious shortage of forage for livestock by consuming plant ma-

terial. The higher temperatures, higher rates of evaporation and lower relative humidity associated with drought are other factors adding to the desiccation problem.

In badly depleted grassland the decade following drought may be characterized by secondary plant succession back towards the climax. This is marked by various stages beginning with a host of annual weeds and ending with the climax species in approximately their original abundance.

During the drought of the 1930's the effects on the Mixed Prairie vegetation decreased northwards from western Kansas. In western Kansas the Mixed Prairie cover was changed into essentially short-grass vegetation by the death of mid-grass dominants. In North Dakota and Montana death of the mid grasses was less common during the shorter period of drought, and in Alberta and Saskatchewan drought was marked, not by death of the mid grasses but, by a reduction in the size of the plants. Recovery from drought was apparently complete by 1944 in the north but was delayed in many other parts until 1950 to 1952 when the next drought started.

In parts of the Great Plains adjacent to more mesic communities an extended period of above-average precipitation may occur without severe drought. Under these conditions the characteristics of the vegetation may be highly modified towards a more mesic type in which the mid grasses play the dominant role.

Many of the studies heretofore carried on in classifying the vegetation of the Great Plains fail to take into account the extent of fluctuations in the vegetation due to changes in weather conditions. A complete description of a vegetation type should include an indication of the extent to which it may progress in the direction of favoring the mid grasses during moist periods and the short grasses during xeric ones. Otherwise the same community may be variously characterized by different workers at different times.

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GENE SEGREGATION IN AUTOTETRAPLOIDS. II

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In 1945 the writer reviewed the literature on segregation in autotetraploids up to that time (53). It was pointed out in that review that there are three main theories regarding autotetraploid segregation. One of these, propounded by Muller (59), is generally referred to as random chromosome segregation; the second, by Haldane (29), as random chromatid segregation. The third, propounded by Mather (57), takes into consideration the amount of quadrivalent formation and the amount of crossing-over between the gene in question and the centromere. Mather also gave a method for calculating a value *alpha*, a measure of the amount of double reduction resulting from crossing-over between two chromatids passing to the same pole in the first meiotic division. The present review will include only the literature published since 1944, with the exception of a few papers of fundamental importance necessary for the understanding of recent reports, and a few papers which were not included in the previous review because at the time they seemed irrelevant to the subject but have assumed some importance in relation to later work.

In the past 12 years there have been no basic changes in the general theory of autotetraploid segregation. There has been published, however, a considerable body of new data, but it is rather surprising, in view of the large number of tetraploids that have been artificially produced, that the number of cases of clear-cut data on genetic characters is rather small. The difficulties of obtaining large populations due to the partial sterility of many tetraploids still stands in the way of accumulating such data. One of

the most striking advances has been made in studies on the behavior of incompatibility factors in autotetraploids as compared with their diploid ancestors.

THEORETICAL TREATMENTS

Bennett (7) considered random mating in populations of organisms exhibiting tetrasomic and hexasomic inheritance with linked factors. He established formulae to describe the equilibrium reached in such populations. Li (47a) has recently discussed methods for partitioning the genotypic variance of an autotetraploid random mating population with random chromosome segregation.

Fisher (21) gave formulae for calculating genotype frequencies, making allowance for double reduction, and also gave a general treatment for linkage in polyploids (22). He applied these linkage formulae to actual data from a natural tetraploid, *Lythrum salicaria* (23).

Geiringer (26) likewise gave a mathematical treatment of linkage in autopolyploids, and of chromatid segregation in autotetraploids and autohexaploids (25).

An important contribution to the classification of polyploids and a clarification of terms has been made by Stebbins (76, 77). For example, the confusion over the terms "autosyndesis" and "allosyndesis" referred to by the writer (53), has been resolved by giving these terms a stricter definition and introducing the designations "homogenetic" and "heterogenetic" association. In regard to the classification of polyploids, Stebbins has established a new class known as "segmental allotetraploids," intermediate between true autotetraploids and allotetraploids. He is of the opinion that many of the naturally occurring polyploids once classified as autotetraploids should be considered in this class. He further points out that tetrasomic segregation alone does not provide conclusive evidence of autopolyploidy. A segmental allotetraploid can display both tetrasomic and disomic segregation.

Paddock (62) points out that in breeding crop plants, autotetraploids should have a theoretical advantage when trying to introduce a single desirable chromosome into a commercial variety. The probability of introducing such a chromosome is increased by using tetraploid times diploid backcrosses instead of the usual diploid times diploid crosses.

NEWLY REPORTED CASES OF TETRAPLOID SEGREGATION

Alfalfa

The exact nature of the polyploidy in cultivated alfalfa, *Medicago sativa*, is still uncertain. Armstrong (2) states that "Cytological and genetic evidence points to tetraploid alfalfa as originating as an alloploid from closely related diploid species." The fact that the hypothetical parent species are specified as being closely related would seem to imply that the parental genomes possess in common a considerable number of chromosome segments or even whole chromosomes. If this is correct, alfalfa should be referred to, according to Stebbins' classification, as a segmental allotetraploid.

On the other hand, Grun (28) states that "Cytological evidence strongly suggests that cultivated alfalfa is an autotetraploid. The genetical ratios reported are, however, almost entirely those to be expected from an alloploid".

Bolton and Greenshields (9) claim to have found a diploid form of *Medicago sativa* from Russia. They felt that the relationship with the cultivated strain was very close on the basis of morphology and crossing studies. There has, however, been no report of this diploid form being artificially doubled to determine whether a tetraploid would be comparable to cultivated alfalfa.

Twamley (90), in a doctoral dissertation, described flower color inheritance in diploid and tetraploid alfalfa. Apparently he was also working with a strain which he considered to be the diploid relative of the cultivated form. The writer was unable to obtain the original dissertation for critical review.

Tysdale, Kiesselbach and Westover (91) considered that some of the data on inheritance in alfalfa could not be explained satisfactorily except on a tetrasomic basis. They referred to some unpublished data by Korohoda dealing with leaf shape. In these data, quadriplex and triplex plants were grouped in one class, duplex and simplex in a second class, and nulliplex plants in a third. The frequencies of these classes were 196, 424 and 28, respectively. Calculating *alpha* gives a value of one-third, indicating the maximum possible amount of double reduction. Based on this value, the expectancies are 192, 424 and 32, a nearly perfect fit to the observed data. The data also fit satisfactorily the expectancies based on random chromatid segregation, though the

deviation from random chromosome segregation is highly significant. The authors point out that these data could not be interpreted on the basis of diploid segregation assuming two, three, or four factors.

Atwood and Grun (5), in their monograph on the cytogenetics of alfalfa, state that at that time no example of segregation existed which could be interpreted only on a tetrasomic basis instead of on either a tetrasomic or a disomic basis. However, they point out that since their review was written, Stanford (75) had reported a clear-cut case of tetrasomic inheritance of flower color.

The genetic evidence alone would strongly support the view that alfalfa is a segmental allotetraploid, since clear-cut cases of both tetrasomic and disomic inheritance have been found[1].

Potatoes

The status of the question regarding the nature of polyploidy in the cultivated potato has not changed appreciably since the work of Cadman (16), although new data on segregation of genetic factors have been published. Fineman (19, 20) explained the inheritance of two types of pollen sterility on a tetraploid basis, enlarging on the early results of Krantz, Becker and Fineman (42). Hutton (35) presented autotetraploid data on factors for response to viruses X and Y. Tetrasomic inheritance of resistance to wart disease was reported by Lunden (55).

Toxopeus and Huijsman (89) studied the inheritance of resistance to root eelworm. This resistance was found in seedlings of *Solanum andigenum* which is probably a subspecies of *S. tuberosum* instead of a distinct species. Crosses among *andigenum* seedlings, involving duplex x duplex, duplex x simplex, and simplex x simplex, all gave satisfactory fits to expectancies based on random chromosome segregation. However, crosses between these seedlings and susceptible commercial potato varieties gave an excess of resistants in eight cases out of nine. Since the first group of crosses was made in the greenhouse under careful control, while

[1] Dudley and Wilsie (17a, b) have recently published data on the inheritance of branched raceme and vestigial flowers. They found that each of the traits was conditioned by four genes, two of which were inherited in a tetrasomic manner while the other two behaved as duplicate disomic genes.

the second group was made in the field where contamination could have occurred, no reliable conclusions could be drawn regarding the differing types of segregation. More carefully controlled experiments reported later by Huijsman (34) showed that the segregations obtained from *andigenum* x *tuberosum* crosses could be explained on the same basis as results from crosses between *andigenum* seedlings.

One line of resistant seedlings was found which gave segregations that could not readily be explained on a tetrasomic basis. These data gave a good fit with ratios expected by assuming two complementary factors with disomic segregation. Swaminathan and Howard (86) reviewed the literature on segregation in potatoes and concluded that most data reported could be interpreted on a tetrasomic basis. In later papers, Swaminathan (84, 85) concluded that "although *Solanum tuberosum* probably arose as an autotetraploid, for all practical purposes, we may consider the current commercial varieties as segmental allotetraploids". Stebbins (76) agreed in referring to the potato as a segmental allotetraploid on the basis of its cytological and genetic behavior but adds that "the case cannot be considered definite until one or both of its diploid ancestors have been indentified".

Since pollen sterility is associated with high yield, Krantz (41) utilized the information on the inheritance of this character in devising breeding methods for obtaining populations with a high proportion of pollen-sterile plants.

Maize

In spite of the fact that autotetraploids of maize have been available for a long time and fertility is reasonably high, virtually no data on tetraploid segregation in this species have been published in scientific journals. Randolph (66) indicated that segregations close to 35:1 have been obtained, but at the time of his review, no large populations had been studied. Welch (92), in an unpublished doctoral thesis, presented data on populations which are probably the largest that have ever been studied with respect to tetraploid segregation. Populations of over 20,000 plants, involving three genetic factors, were studied. Populations totaling about 2,000 plants involved a fourth factor. All four of these factors studied were located in the same chromosome, and their positions

on the chromosome as well as the position of the centromere were well known from studies of diploids. While this study was conducted primarily for the investigation of linkage in an autotetraploid, the segregations of the individual factors were presented in tabular form. The segregations of liguleless, glossy-2 and virescent-4 all deviated significantly from both random chromosome and random chromatid segregation. In the case of the factor B (plant color intensifier), deviations from random chromosome segregation were not significant in backcrosses between duplex or simplex plants and nulliplex plants. However, a cross between triplex and nulliplex gave two recessives in a population of 125 plants. This could have arisen only by double reduction.

The writer has calculated the values of *alpha* from the segregation data for these four factors and compared the values obtained with the known distances of each factor from the centromere (Table I).

TABLE I

AMOUNT OF DOUBLE REDUCTION (ALPHA) EXHIBITED IN SEGREGATION OF FOUR GENES IN MAIZE, COMPARED WITH THEIR POSITIONS ON THE CHROMOSOME. (FROM DATA BY WELCH (92))

Gene Locus	Alpha	Crossover Units From Centromere
Lg	.228±.017	66
Gl_2	.215±.017	47
B	.109±.050	28
V_4	.086±.016	6

It can be seen from the table that the order of magnitude of double reduction as indicated by the values of *alpha* is the same as the order of magnitude of the crossover distances from the centromere.

Lythrum salicaria

Studies on the inheritance of style length have been continued by Fisher (23) as well as on a pair of factors for purple (R) versus rosy (r) located on the same chromosome. Linkage studies

were also carried out between these two factors. At first the amount of double reduction at the r locus was calculated to be about 6%. A later paper by Fisher and Fyfe (24) showed that the original estimate of double reduction was high and pointed out that contaminations can badly distort the results in studies of tetraploid segregation when only small numbers are expected.

Spinach

In diploid spinach it has been shown that sex is determined by a single pair of factors designated as X and Y. Plants homozygous for X are pistillate, while those containing one or two Y genes are staminate. Janick and Stevenson (37, 38) showed that in tetraploids, a single Y gene causes the plant to be staminate, even in combination with three X genes. They presented genetic evidence to show that pairing and disjunction of chromosomes containing the X and Y factors are completely at random in tetraploid and triploid. Thus duplex plants crossed with pistillate plants give ratios of approximately 5 staminate: 1 pistillate. Janick (36) published more extensive data and concluded that segregation "is typical of chromosome segregation as constrasted to chromatid segregation in a duplex backcross." This statement was hardly borne out by the data, since a total of 378 staminate to 93 pistillate plants was obtained. The chi-square value based on chromosome segregation was 3.21, while for chromatid segregation it was .79. The author points out that the elimination of one progeny suspected of being contaminated would result in almost perfect fit with the expected chromosome segregation.

Phleum pratense

The nature of polyploidy in cultivated timothy has been the subject of many investigations, both genetic and cytological. Earlier workers generally considered it to be an autohexaploid, but Stebbins (76), in reviewing recent work on the subject, considers the cytological evidence as favoring the view that it is an auto-allohexaploid with four genomes derived from one parent species and two from another. Nordenskiöld (60) analyzed the genetic segregations in large populations segregating for white seedlings. She compared the data with three sets of expectancies based on (*a*) disomic segregation of three pairs of independent factors, (*b*)

tetrasomic segregation for a locus on four homologous chromosomes and disomic segregation of an independent factor pair, and (*c*) hexasomic segregation based on random pairing among six homologous chromosomes. She found that all of her data fit the hypothesis of hexasomic segregation satisfactorily and that many of the populations studied deviated significantly from one or both of the other hypotheses. This indicated that at least the six chromosomes containing the locus for white seedlings were sufficiently homologous to pair at random. Recently, Nordenskiöld (60a) has shown that hexasomic ratios are also obtained when a synthesized form of *Phleum pratense* is crossed with the natural form.

Rice

The segregation ratios of colored versus colorless glume tips in autotetraploid rice hybrids were examined by Morinaga (58). He found that in the F_2 generation the data approximated the theoretical ratio expected on the basis of random chromatid segregation, while F_3 data fit more closely the expectancies based on random chromosome segregation. However, the writer has calculated the value of *alpha* from Morinaga's data and found it to be 0.18, and on calculating expectancies based on this value, it is found that all of the data give a satisfactory fit. This example brings out a point which the writer tried to emphasize in his earlier review (53), namely, that the practice of fitting data to either of the two limiting ratios known as "chromosome" and "chromatid segregation" is often meaningless. Nearly all segregating progenies in autotetraploids will exhibit ratios somewhere between these two limits, and the important problem is to determine what has been the extent of double reduction, caused by quadrivalent formation and crossing-over between the gene and the centomere, as measured by *alpha*.

Canna

Oomen (61) gave data on progenies from hybrids of autotetraploid *Canna*, but the populations were far too small to draw any conclusions regarding the nature of segregations. He observed that the range of colors in the tetraploids was greater than in the diploids, probably due to the greater number of genotypes possible at each locus.

Yeast

In cultures of various species of *Saccharomyces*, zygotes which are heterozygous for a given gene are normally expected to produce asci containing four spores with a ratio of 2:2 dominants to recessives. Occasional deviations from this ratio are encountered, the most common being 4:0 and 3:1, and more rarely 1:3 and 0:4. Polyploidy has been shown to contribute to these irregular ratios in many cases (Lindegren and Lindegren (50); Roman, Hawthorne and Douglas (69); Leupold and Hottinguer (43); Roman (68); Roman, Phillips and Sands (70); Pomper, Daniels and McKee (65); and Hawthorne (30).

Winge and Roberts (93) proposed a non-tetraploid explanation for these irregular ratios, based on their observations of occasional 8-nucleate asci resulting from a post meiotic division. They pointed out that irregular ratios would result if the four spores in an ascus were the survivors of a larger number (usually eight spores).

Irregularities which could not be explained readily on a tetraploid basis were also found by Lindegren (48). He proposed a theory of gene conversion, a special type of mutation theory in which recessive genes are caused to mutate in the presence of their dominant allele.

Both of these theories were opposed by Ranganathan and Subramaniam (67) and by Subramaniam (82) who cautioned against "offering radical theories to explain curious segregations observed in hybridization experiments" (67). Still, both Lindegren (49, 50, 51) and Winge and Roberts (94) later presented additional evidence in support of their theories[2]. In reviewing the whole subject, Roman, Phillips and Sands (70) concluded that irregular segregations could arise from several causes, but that in most cases, polyploidy offered the most satisfactory explanation.

Hawthorne (30) showed that the order of spores in linear asci could be used for estimating the linkage between a gene and the centromere in diploid populations. He obtained such an estimate for linkage between the tryptohane locus and the centromere from

[2] Winge and Roberts (95) have again replied to their critics, maintaining that none of the data so far presented is in disagreement with their theory on post meiotic divisions as being one of the central causes of irregular ratios.

the analysis of linear asci in a diploid hybrid. He applied this estimate to tetraploid data and found a satisfactory agreement between observed and expected segregation, although the populations studied were rather small. Of the seven genes which he studied, the other six displayed no linkage with the centromere, indicating that these loci were probably far removed from the centromere with a high frequency of crossing-over between them.

Roman, Phillips and Sands (70) gave more extensive data for tetraploid segregations and derived two sets of equations for calculating expectancies; one of these was based on bivalent pairing and the other on quadrivalent[3] pairing with random disjunction of the centromeres at the first division. These two are special cases of a more general set of equations derived by the writer. Designating 4:0 asci as Type I, 2:2 asci as Type II, and 3:1 asci as Type III, these equations for the frequencies of the three types are as follows:

$$f(I) = (4 - 4x + 3x^2 - 2ax^2)/6$$
$$f(II) = (2 - 4x + 3x^2 - 2ax^2 + 4ax)/6$$
$$f(III) = (4x - 3x^2 + 2ax^2 - 2ax)/3$$

where x is the percent of second division segregation (called e by Mather (57)) and a is the percent of genetic non-disjunction. When a is zero, these equations become those given by Roman, et al. for bivalent pairing. When a is 1/3, they give those for quadrivalent pairing.

From the above formulae, it is also possible to derive two equations for calculating values of a and x from observed data:

$$(1) \qquad ax = alpha \text{ (Mather)} = \underline{/}\overline{1\text{-}3\,(f(I) - f(II))}\underline{/}\overline{\ /2}$$

$$(2) \qquad x = \underline{/}\overline{(2 + alpha) \pm \sqrt{(2 + alpha)^2 - 6(2 - 3f(1))}}\underline{/}\overline{\ /3}$$

Thus, from tetrad analysis in tetraploid yeasts, information can be obtained regarding the amount of crossing-over between a gene and its centromere (x/2) and also the type of pairing and disjunction of chromosomes (a). However, these estimates have the following limitations:

[3] The authors cited used the term "tetravalent", but the writer has used the more generally accepted "quadrivalent" which is etymologically preferrable.

a) Since two values are computed from three frequencies whose total is fixed, there are no degrees of freedom for estimating standard error. In other words, using these values for calculating expectancies will always give a perfect fit to the observed data.

b) Equation (2) will usually have two roots, both of which may fall in the interval from 0 to 1.

c) Equation (2) will have imaginary roots if the portion under the radical is negative, in which case, that portion of the equation must be disregarded.

All of the spores from Type I tetrads and half of those from Type III are heterozygous, while each of the homozygous classes is made up of half the spores from Type II tetrads and one fourth of those from Type III. Taking these facts into account, the total frequency of heterozygous spores is seen to be $(4 - 2\ alpha)/6$, and that of each of the homozygous classes is $(1 + alpha)/6$. These are the same frequencies given by Mather (57) for gametes from a duplex autotetraploid in flowering plants. This emphasizes the point that tetrad analysis in tetraploid yeasts and other fungi can furnish information as to the separate effects of a and x on segregation, while data on total spore frequency alone can furnish information only on the combined effect of these two variables.

Analysis of asci from simplex zygotes was also carried out by Roman et al. (70), and 1:3 asci were found in such populations. It was shown that this type of ascus could arise only through double reduction, resulting in one of the spores receiving both of the sister chromatids bearing the dominant allele.

SEGREGATION AND ACTION OF INCOMPATIBILITY GENES IN AUTOTETRAPLOIDS

Some of the most extensive work in the field of autotetraploid genetics in recent years has dealt with the behavior of genes for incompatibility in tetraploids as compared with diploids. General reviews of the literature on incompatibilty in diploids and tetraploids were presented by Lewis (44, 46), and more recently a concise summary of the published results in autotetraploids appeared in a monograph by Atwood and Brewbaker (4).

The genetic mechanisms controlling incompatibility in diploids fall into two general types. The more common of these appears to

be the S allele or personate type in which the reaction of the pollen is determined gametophytically or by the alleles in the pollen. Other systems, such as the "Capsella type" and the R alleles, comprise a general type in which the reaction of the pollen is sporophytically determined, that is, by the genotype of the style. It would be expected that with either of these types of incompatibility, inheritance in tetraploids would be greatly complicated for two reasons. First, in a tetraploid, heterogenic pollen is possible, whereas in the diploid each pollen grain carries only a single allele at each locus. Second, the number of possible genotypes in the sporophyte is greatly increased in tetraploids. Thus, with four alleles, only ten genotypes are possible in diploids, while 35 are possible in tetraploids. Atwood (3) established the necessary terminology to cope with this complexity of genotypes in tetraploids. The terms he suggested, which are self-explanatory, were "monoallelic," "balanced diallelic," "unbalanced diallelic," "triallelic" and "tetraallelic." Pollen is referred to as homogenic or heterogenic, according to whether the two alleles it contains are alike or different.

One of the most striking results of chromosome doubling in plants containing the S alleles is the phenomenon known as "competition", first described by Lewis and Modlibowska (47) in connection with studies on fertility in tetraploid pears. It was found that certain heterogenic combinations will enable the pollen to function even on styles containing both of the pollen alleles, and it was believed that in some way, these two alleles tend to nullify the inhibiting effect of each other. Lewis (45) found further evidence in support of this hypothesis in studies with *Oenothera*. The same phenomenon was found by Atwood and Brewbaker (4, 12, 14) in autotetraploid white clover (*Trifolium repens*). The functioning of competition pollen can result in the production of self-compatible tetraploids directly from self-incompatible diploids. For example, if pollen with the genotype S_1S_2 displays competition, tetraploids with the genotype $S_1S_1S_2S_2$ will be self-compatible, but their diploid progenitor with the genotype S_1S_2 will be self-incompatible.

Another phenomenon, impossible in diploids, is that of dominance, first described by Lewis (45). In this case, one of the alleles in a heterogenic pollen grain, referred to as the "dominant allele", will suppress the inhibiting effect of the other or recssive

allele. Thus, if S_1 is dominant over S_2, an S_1S_2 pollen grain will not function in a style containing an S_1 allele but will function in a style which contains an S_2 allele, provided no S_1 alleles are present. It will be noted that, unlike the case of competition, dominance cannot result in the production of self-compatible autotetraploids. Atwood and Brewbaker (4) studied the dominance relations of four S alleles in white clover and found that these alleles could be arranged in a linear order as regards dominance. They also observed that the degree of dominance varied and was never complete. The following interesting comment appears regarding the concept of dominance from the standpoint of theoretical genetics: "In haploid pollen, under a personate system, there is no opportunity for dominance to be expressed, and selective pressures have no chance to influence the evolution of dominance patterns. Even so, when the 32-chromosome white clover was doubled with colchicine, a well-defined series of dominance relationships appeared immediately in the diploid pollen. This suggests that dominance is a basic characteristic of S alleles and may evolve in the absence of selective influence."

Further studies with white clover by Brewbaker (13) revealed that the dominance relations of another set of four S alleles could not be represented in a linear system, since every one of the four alleles was dominant over at least one of the other three. He showed, moreover, that some of the genotypes in his progenies could not be accounted for on the basis of either dominance or competition. Although the earlier paper by Atwood and Brewbaker (4) had stated that the data gave more satisfactory fits to chromosome segregation than to chromatid segregation, these new results could be explained only on the basis of pollen grains formed by double reduction. Sufficiently large populations were obtained to calculate a value of *alpha*, and it was concluded that the amount of crossing-over between the S alleles and the centromere was at least 22 units. Recalculating the expectancies on this basis led to a satisfactory fit for the data in both the current study and the earlier studies.

Other species of *Trifolium* which have been studied with respect to the behavior of S alleles in tetraploids have been *T. hybridum* (alsike clover) (Brewbaker, 10, 11) and *T. pratense* (red clover)

(Pandy, 63). The results have been similar to but not so extensive as the results with white clover.

Other studies on the effects of tetraploidy on the action of S alleles have given a wide range of results. In *Petunia*, Stout and Chandler (79), Stout (78) and Straub (81) all found that self-sterile diploids became self-fertile after chromosome doubling. Atwood and Brewbaker (4) have suggested that these cases may be due to the functioning of competition pollen grains, as had been demonstrated in *Oenothera* and *Trifolium* and suspected in *Pyrus*.

At the other extreme, Hecht (31, 32) found that self-sterile plants of *Oenothera rhombipetala* remained self-sterile after doubling. Lewis (44) found the same situation in *Oenothera organensis*, but also noted some plants of this species in which the inhibition of pollen tube growth was weakened, although not sufficiently to allow fertilization.

The other general type of incompatibility, where the reaction of pollen is sporophytically determined, is common in the Cruciferae. The situation in polyploids of this family was reviewed by Batemen (6). He pointed out that, although in other families there are many cases of self-sterile plants becoming self-fertile after doubling, this is generally not true of crucifers, where pollen reaction is sporophytically determined. Results obtained by Howard (33) with *Brassica* and *Raphanus* were cited in support of his conclusion. More recent studies by Shibata (72, 73) with *Brassica pekinensis* have likewise produced no examples of changes from self-sterility to self-fertility after doubling. He did, however, find examples of dominance, as for example, in crosses between $S_1S_1S_1S_1$ and $S_1S_1S_2S_2$, where it was found that both S_2S_2 and S_1S_2 pollen would function. Plants of the type $S_aS_aS_aS_b$ were always incompatible when pollinated with $S_aS_aS_aS_a$ plants but were compatible with $S_bS_bS_bS_b$, although $S_cS_cS_cS_c$ gave a still better set of seed. In view of the fact that S_bS_b pollen grains evidently function on $S_aS_aS_aS_b$ styles, it would be expected that $S_aS_aS_aS_b$ plants should produce some seed on selfing if S_bS_b pollen grains are produced by double reduction. Apparently this idea has not been tested.

Contrary to the above cited results, Straub (80) found that self-sterile plants of kohl-rabi (*Brassica oleracea* var. *gongylodes*) be-

came self-fertile after doubling with colchicine. He suggested as explanations the dilution of inhibiting substances in the larger volume of the tetraploids or the occurrence of new no-stopping combinations of sterility alleles. Bishop (8) found both self-sterile and self-fertile plants in an F_2 of autotetraploid broccoli. He also reported differences in reciprocal crosses, as did Shibata. In none of the studies with crucifers have the populations been large enough to draw any conclusions as to segregation ratios, and no clear cut cases of double reduction have been established.

The remainder of the studies on self-incompatibility in tetraploids have dealt with species in which the system of inheritance in the diploids has not been firmly established. Livermore and Johnstone (54) found that self-sterile plants of *Solanum bulbocastanum* became self-fertile upon doubling. Swaminathan (83) and Torka (88), in studies with *Solanum chacoense,* and Straub (80, 81) with *Antirrhinum glutinosum* and *A. molle*, met the same situation. In rye, Lundquist (56, 56a) observed that self-incompatibility was somewhat "weakened" in tetraploids.

GENERAL FERTILITY OF AUTOTETRAPLOIDS

One of the serious difficulties encountered in the genetic analysis of autotetraploids is their low fertility. The writer (52) found that fertility in autotetraploids of *Antirrhinum majus* could be increased markedly by selection in a few generations. These tetraploids are now widely grown by florists and gardeners, and it has been the experience of seedsmen that yields of seed have substantially increased over those obtained in the original strains, either through natural or artificial selection for high fertility.

Similar increases in fertility have been observed in other new autotetraploids. Alcarez and Tamayo (1) found that fertility was very low in new tetraploids of *Nicotiana* but was increased greatly by selecting until the fourth generation, after which it was quite stable. Gilles and Randolph (27) increased the fertility in a line of autotetraploid maize by ten years of selection, and found that the average number of quadrivalents per cell decreased from 8.47 to 7.46 during this period. They concluded that quadrivalent frequencies are of doubtful value in classifying old polyploids.

Some evidence that selection does not always reduce quadrivalent frequency was obtained by Brown, Ponewczynski and Scar-

borough (15) in studies with *Tradescantia reverchoni*, an old autotetraploid with no known diploid forms. In spite of the fact that this species must have been subjected to many generations of natural selection, 55.5% of the chromosomes are involved in quadrivalent formations.

Kadota and Ito (39) were able to increase both the self-fertility and the general fertility of autotetraploid Chinese cabbage by selection. Differences were recorded in fertility of various lines of autotetraploid *Capsicum annuum* by Kedharnath and Parthasarathy (40), and they obtained evidence of genetic determiners controlling meiosis and the functioning of abnormal gametes. Increases of fertility by selection have been observed in buckwheat (71) and in eggplant (87).

Einset (18) studied fertility in autotetraploid lettuce and found the aneuploid plants to be more sterile than the euploids. Selection should therefore tend to eleminate the aneuploids and favor increased meiotic regularity.

Since segregation of genetic characters in autotetraploids is affected by cytological behavior, it would be expected that the nature of segregation should change as the result of selection for increased fertility. There seem to be no published experimental results demonstrating such a change in genetic segregation.

PHENOTYPIC EXPRESSION IN AUTOTETRAPLOIDS

With any pair of alleles in a diploid, there are only three possible genotypes, while in an autotetraploid there are five. This condition may lead to new phenotypes in a tetraploid. For example, in tomato, a dominant gene, "wooly," causes heterozygous plants to be wooly but is lethal in the homozygous condition. Thus there are only two phenotypes, wooly and non-wooly. Soost (74) found that four classes could be distinguished in the tetraploids. The nulliplex plants were non-wooly, while the simplex, duplex and triplex plants showed an increase in wooliness with gene dosage. These three types were normal in growth and fertility, indicating that even three wooly genes did not exert a lethal effect in the presence of a single non-wooly gene. The quadriplex was not recovered, and this combination is presumably lethal as in the homozygous diploid.

If more than two alleles exist at a locus, the increase in pheno-

types is even more pronounced. With three alleles the numbers of genotypes in diploids and tetraploids are six and fifteen, respectively. With four alleles, these values become ten and thirty-five. This increase in genotypes has been observed in connection with sterility alleles discussed earlier.

Further general discussions on the phenotypic expression of genes in autotetraploids are given by Crane and Lawrence (17) and by Pirschle (64).

SUMMARY

Extensive data on segregation of genetic characters in autotetraploids have been obtained for 12 genera representing eight families of flowering plants and one family of fungi. Eight of these genera are *Primula*, *Datura*, *Solanum*, *Lycopersicum*, *Dahlia*, *Rubus*, *Lythrum* and *Antirrhinum*, covered in the first review. Data on *Zea*, *Oryza*, *Trifolium* and *Saccharomyces* are covered in the current review. In all of these cases, the phenomenon of double reduction has been demonstrated, so that the general principles of autotetraploid segregation have been firmly established in a wide range of plant families.

In addition to the 12 genera mentioned above, less extensive data have been presented on *Lotus*, *Medicago*, *Spinacia*, *Canna*, *Pyrus*, *Phleum*, *Oenothera*, *Petunia*, *Brassica* and *Raphanus*. This later group represents four additional families.

There have been two outstanding advances in the field of autotetraploid genetics since publication of the previous review. The first of these has been concerned with the genetics of autotetraploid yeasts. In this plant the analysis of tetrads has made possible the securing of more detailed information on the behavior of genetic factors during meiosis in autotetraploids. The second big advance has dealt with the segregation and behavior of incompatibility alleles in flowering plants. The most thorough analysis of this type has been carried out with *Trifolium repens*.

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